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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.

DISTRIBUTION OF LARVAL TUNAS IN MARQUESAN WATERS

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ABSTRACT

Spawning of tunas near the Marquesas Islands was investigated by studying the distribution of larval tunas collected in 1957 and 1958. Of the six species of larval tunas identified, larval skipjack (*Katsuwonus pelamis*) occurred most frequently. Prominent diel variation with greater catches at night was observed at a station occupied for 24 hours in December 1957 and March 1958 for larval skipjack and in January 1958 for larval yellowfin (*Thunnus albacares*). Both the incidence of the capture of larval tunas and their abundance were greater during the southern summer and fall (January to April) than in the other months of the year. There was no difference in abundance of larval tunas with respect to distance from shore, nor were there any differences in abundance among the four transects (north, east, south, and west of the islands) along which sampling was conducted. No significant correlation was found between abundance of invertebrate plankton and larval tunas nor between schools of adult tunas sighted and abundance of larval tunas. Temporal distribution of larvae indicated some spawning by skipjack throughout the year.

Oceanographic and fishing surveys in the Pacific near the Marquesas Islands (fig. 1) during 1957–58 were part of a program undertaken by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, to investigate the tuna resources in this area. Pertinent to this investigation was a study of the time and location of the spawning of tunas.

Methods of determining spawning activities of tunas involve inferences from studies of their ovaries and the distribution of their larvae. The latter method has been made possible by the identification (tentative for some species) and detailed descriptions of the larvae of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*), albacore (*Thunnus alalunga*), bluefin (*Thunnus thynnus orientalis*), longfin (*Thunnus tonggol*), three species of *Euthynnus*, and *Auxis* sp. (Matsumoto, 1958, 1959, 1962; Mead, 1951; Wade, 1951). Attempts to identify specifically eggs of these tunas have been unsuccessful because of their similarity

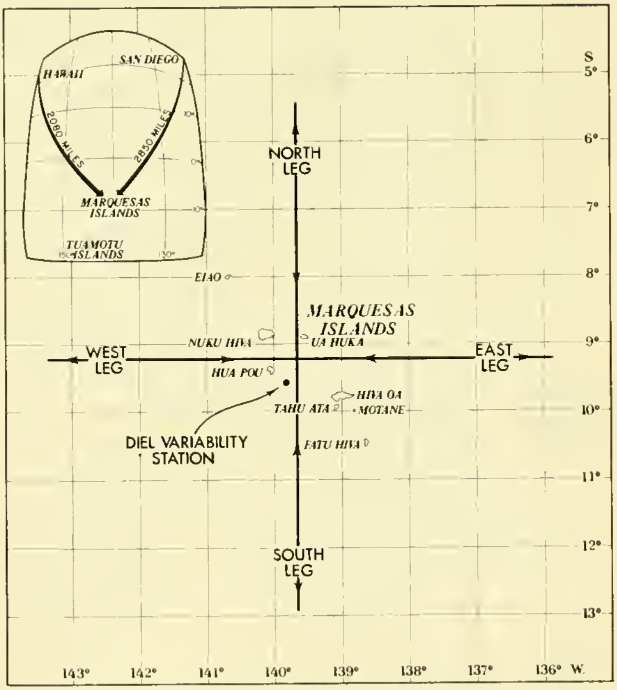

Figure 1.—Offshore survey track and the diel variability station in the Marquesas, 1957–58.

Note.—Approved for publication October 12, 1965.

in appearance and the overlapping ranges of their diameters (Matsumoto, 1958).

This report presents information on the abundance and distribution of larval tunas in the region of the Marquesas Islands. Six species of larval tunas were identified, but emphasis is on skipjack, as it occurred more often than the others. Inferences concerning skipjack spawning are compared with those derived from ovarian studies of this species from the same area (Yoshida, 1965).

COLLECTION OF SAMPLES

Plankton samples from which the larval tunas were sorted and counted were collected from research vessels of the Bureau of Commercial Fisheries in 1957 and 1958 on a standardized offshore survey pattern and at a diel variability station (fig. 1). The latter was situated at lat. 9°34′ S. and long. 139°50′ W. (about 15 miles southeast of the island of Hua Pou) and was occupied for 24-hour periods on six occasions. Cruises, dates, and numbers of samples obtained on the offshore surveys and at the diel variability station are summarized in tables 1 and 2 respectively. Fishery and environmental data collected on these cruises have been published by Wilson, Nakamura, and Yoshida (1958).

Plankton hauls were made with a net having a mouth diameter of 1 m. The net was constructed of nylon netting with mesh apertures of 0.66 mm. in the body and 0.31 mm. in the rear and cod end (for details of construction and dimensions, see King and Demond, 1953). A flowmeter mounted in the center of the mouth provided estimates of the amount of water strained.

Table 1.—*Cruises, dates, and numbers of zooplankton samples obtained on offshore surveys* [*CHG* = Charles H. Gilbert, *HMS* = Hugh M. Smith]

Cruise	Dates	Number of samples
CHG-35	Oct. 24-Nov. 7, 1957	46
HMS-43	Jan. 27-Feb. 12, 1958	22
CHG-38	Mar. 26-Apr. 9, 1958	24
HMS-45	May 15-May 30, 1958	21

Table 2.—*Cruises, dates, and numbers of zooplankton samples obtained at the diel variability station* [*CHG* = Charles H. Gilbert, *HMS* = Hugh M. Smith]

Cruise	Dates	Number of samples
CHG-35	Oct. 21-22, 1957	16
CHG-35	Dec. 1-2, 1957	16
HMS-43	Jan. 23-24, 1958	12
CHG-38	Mar. 6-7, 1958	12
CHG-38	Apr. 17-18, 1958	12
HMS-45	June 8-9, 1958	24

Oblique, open-net, ½-hour plankton hauls from the surface down to 140 m. and back to the surface were taken during the offshore surveys and at the diel variability station on all cruises. A second net was attached to the towing cable to permit sampling between 140 and 280 m. at the diel variability station on *Hugh M. Smith* cruise 45 (HMS–45). This latter net was similar to the open one but was modified to permit attachment of opening and closing devices (King, Austin, and Doty, 1957).

Two consecutive ½-hour tows were made during *Charles H. Gilbert* cruise 35 (CHG–35) to obtain data for testing the duplicability of the catches.

On the offshore surveys, plankton hauls were made twice each night, once before midnight (between 2000 and 0000 hours) and once after midnight (between 0200 and 0400 hours). At the diel variability station, duplicate hauls were made every 3 hours on CHG–35, while single hauls were taken at 2-hour intervals on the other cruises.

Plankton samples were preserved in 10 percent Formalin.[1]

In the laboratory all fish and fish eggs were sorted from plankton samples with the aid of binocular dissecting microscopes. From these collections of fish and eggs, larval tunas were separated and identified. Most of the larvae were less than 5 mm. in total length. Specimens greater than 10 mm. comprised a very small percentage of the total number.

TREATMENT OF DATA

Larval abundance is expressed as the number of larvae in a column of water 10 m. square and 140 m. deep. This value was obtained by multiplying the number of larvae per cubic meter of water strained by the volume of the column of water.

Nonparametric statistics (Siegel, 1956) were used in our analyses to avoid assumptions of normal distributions.

Data on plankton hauls and numbers of larval tunas collected at the diel variability station and on the offshore surveys are presented in appendix tables A–1 through A–8.

DUPLICABILITY OF CATCHES

Catches of larval tunas by successive tows were compared by Strasburg (1960). He found no significant difference and concluded that plankton nets were reliable tools for sampling larval tunas within the limitations of the method. All of his tows were taken at the surface and at night.

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

To determine if catches could be duplicated during other hours and with oblique tows, the data from the 39 pairs of plankton tows taken during CHG–35 were examined. The abundance of larval tunas calculated from catches of the first tow did not differ significantly (Wilcoxon matched-pairs signed-ranks test) from that of the second. We thus concluded that catches by oblique tows taken during day or night were duplicative.

SPECIES COMPOSITION

Larvae of the following species of tunas were identified in the Marquesan samples: skipjack, yellowfin, bigeye, albacore, little tunny (*Euthynnus affinis*), and frigate mackerel (*Auxis* sp.)[2]. Adults of all except *Auxis* have been caught either by longline, trolling, or pole-and-line fishing in the Marquesas (King et al., 1957; Austin, 1957; Wilson and Rinkel, 1957; Wilson et al., 1958; Yoshida, 1960). Another species, the dogtooth tuna (*Gymnosarda nuda*), also has been caught in the Marquesas by trolling near the islands, but its larva has not been identified.

The species composition of the larval tunas is shown in table 3. Skipjack was the dominant species throughout the offshore surveys and at all but one of the diel variability stations. At the diel variability station occupied during HMS–43, yellowfin was dominant (appendix table A–2). Other species were found in sporadic abundance, e.g., *Auxis* at the second diel variability station of CHG–35 (appendix table A–1), bigeye at the diel variability station of HMS–43 (appendix table A–2) and on the offshore surveys of CHG–38 (appendix table A–7) and HMS–45 (appendix table A–8).

TABLE 3.—*Species composition of larval tunas collected in Marquesan waters, 1957–58*

Species	Diel variability station		Offshore surveys	
	Number collected	Percent of total catch	Number collected	Percent of total catch
K. pelamis	351	63.8	472	83.0
T. albacares	63	11.5	19	3.3
T. obesus	30	5.5	41	7.2
T. alalunga	3	0.5	8	1.4
E. affinis	2	0.4	0	0
Auxis sp.	80	14.5	10	1.8
Unidentified tuna	21	3.8	19	3.3
Total	550		569	

DIEL AND SEASONAL DISTRIBUTION

Diel variation in catches of larval tunas has been discussed by Wade (1951), Matsumoto (1958), and Strasburg (1960). All reported greater catches at night. The latter two authors attributed this primarily to vertical migration by the larvae into the upper surface layers of the ocean at night, although they did not rule out the possibility of net dodging during daylight.

Since Strasburg (1960) found practically no larval tunas below 140 m., our sampling did not extend below this depth (except at the diel variability station on HMS–45). By sampling the 0- to 140-m. depth range, we hoped that variations due to diel vertical migration would be kept to a minimum or even possibly eliminated.

Catches at the diel variability station during CHG–35, HMS–43, and CHG–38 provided evidence that this variation was not eliminated. Prominent diel variations occurred in December and March for skipjack and in January for yellowfin (fig. 2). Either the larvae did occur below 140 m., or they were more successful in escaping the net during the day in these instances. The problem of diel variation was complicated further by the inconsistency of the catches during the other months. For example, the highest catches of larval skipjack were obtained during or near twilight in April and June, while during October and January day catches were as good as night catches.

Average larval abundance during the offshore surveys of each cruise was compared with those of the other cruises for seasonal variation (fig. 3). The abundance during HMS–43 (January to February) and during CHG–38 (March to April) was significantly greater (Mann–Whitney U test, $p<0.05$) on both occasions than for either HMS–45 (May) or CHG–35 (October to November). No significant differences were found in other comparisons of offshore averages.

Averages for the diel variability station, computed from results of tows taken between 2000 and 0400 hours, the same hours during which tows were taken on the offshore surveys, also are shown in figure 3. The magnitudes and variations of these averages differ considerably from those of the offshore surveys.

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[2] May include both *A. thazard* and *A. rochei* (=*A. thynnoides*); see Matsumoto (1959).

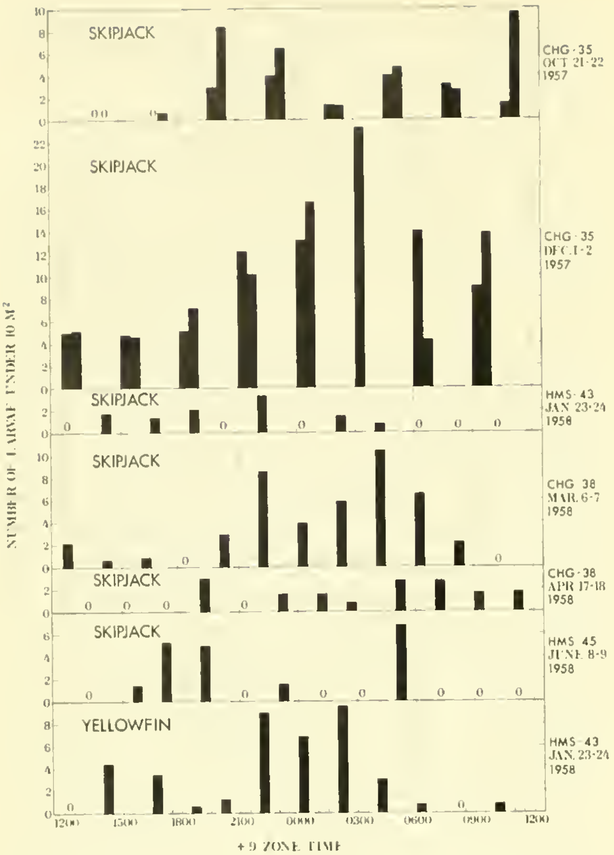

FIGURE 2.—Diel variation in abundance of larval skipjack and larval yellowfin.

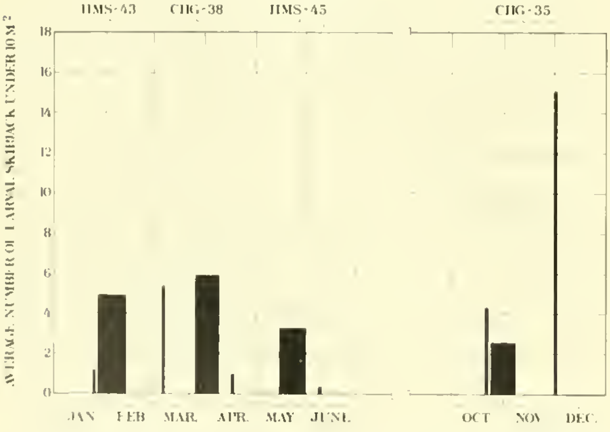

FIGURE 3.—Seasonal variation in the abundance of larval skipjack. The slender bars represent averages for the diel variability station, the thick bars averages for the offshore surveys.

The averages for the offshore surveys represent more samples and a greater areal and temporal coverage than those for the diel variability station. Based on the offshore data, skipjack spawning appears to be greater during the southern summer (January to February) and early fall (March to April), but paucity of data during the southern winter and spring (June to October) makes this conclusion tenuous.

VERTICAL AND HORIZONTAL DISTRIBUTION

Strasburg (1960) observed that most larval tunas were captured within the upper 60 m. of water, with 20 to 25 percent of the catch within the 70- to 130-m. depth, and practically none below 140 m. Since the possibility of larval tunas in waters below 140 m. had been indicated in the earlier cruises (fig. 2), special plankton hauls were planned for the diel variability station during HMS–45. A closing net of dimensions similar to those of the open net was added to the towing cable to permit sampling at depths between 140 and 280 m. Although simultaneous sampling was planned for depth ranges of 0 to 140 and 140 to 280 m., the actual maximum depth sampled by the upper net ranged between 121 and 150 m., while the depths sampled by the lower net ranged between 70 and 262 m. (appendix table A–4).

No larval tunas were caught by the lower net. Larvae were caught only in 6 of the 12 hauls by the upper net. Although the results did not conflict with those of Strasburg, the meager catches and the departures from the planned sampling depths caused the results to be inconclusive.

A relation between larval skipjack distribution and area was not evident. No significant areal association (Kendall coefficient of concordance) was found in the average abundance of larvae for the several legs of the offshore survey track, nor was a relation between larval distribution and proximity to land found in a comparison (Kendall coefficient of concordance) of the average abundance by inner, middle, and outer 75-mile sections of the offshore survey legs (tables 4 and 5).

TABLE 4.—*Average number of larval skipjack under 10 m.² of ocean surface for the north, south, east, and west legs of the offshore surveys (fig. 1).*

[Numbers of samples on which the averages are based are in parentheses]

Cruise	North leg	South leg	East leg	West leg
CHG-35	2.5 (12)	3.3 (10)	0.9 (12)	3.9 (12)
HMS-43	5.9 (6)	5.6 (6)	4.4 (4)	3.6 (6)
CHG-38	11.4 (6)	4.2 (6)	4.0 (6)	3.9 (6)
HMS-45	1.2 (5)	2.5 (6)	8.8 (5)	0.9 (5)

TABLE 5.—*Average number of larval skipjack under 10 m.² of ocean surface for the inner, middle, and outer 75-mile sections of the offshore surveys.*

[Numbers of samples on which the averages are based are in parentheses]

Cruise	Inner 75 miles		Middle 75 miles		Outer 75 miles	
CHG-35	2.3	(14)	2.7	(16)	2.9	(16)
HMS-43	1.9	(8)	6.1	(6)	7.1	(8)
CHG-38	6.2	(8)	5.7	(8)	5.7	(8)
HMS-45	3.2	(5)	4.8	(8)	1.9	(8)

Larval skipjack had been found to be widely distributed in the northeastern part of French Oceania previous to the series of cruises in this report. Figure 4 illustrates the locations around the Marquesas Islands where larval tunas were collected during cruises of vessels of the Bureau of Commercial Fisheries prior to those listed in table 1.

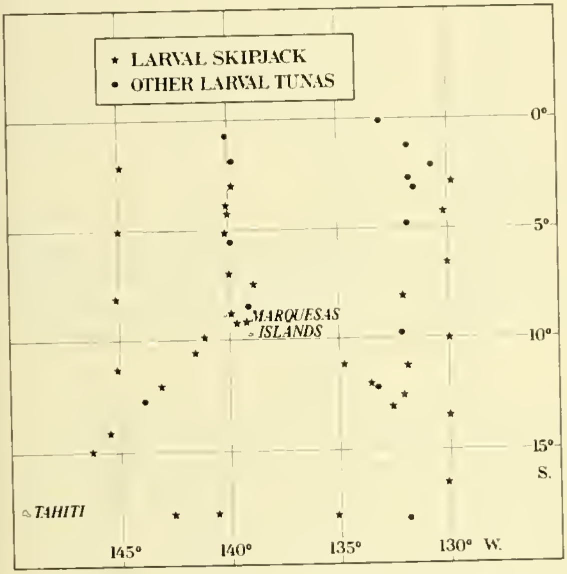

FIGURE 4.—Stations in northeastern French Oceania where larval tunas were collected on cruises earlier (1952–57) than those covered by this study. (Data from Matsumoto, 1958, and Strasburg, 1960.)

ABUNDANCE OF LARVAL TUNAS AND INVERTEBRATE PLANKTON

Relations between the abundance and distribution of invertebrate plankton and of larval tunas, if any exist, are obscure. If the plankton volumes and abundance of larval tunas are averaged for each of the offshore surveys, an obvious positive correlation can be seen (fig. 5), but in individual samples no significant correlations (Spearman rank correlation) were found. High and low measures of abundance of larval tunas were found in high as well as in low volumes of plankton. Strasburg (1960) reported that high catches of larval tunas came from samples of low and moderate volumes of plankton, while the samples with lowest and highest plankton volumes contained smaller numbers of larval tunas.

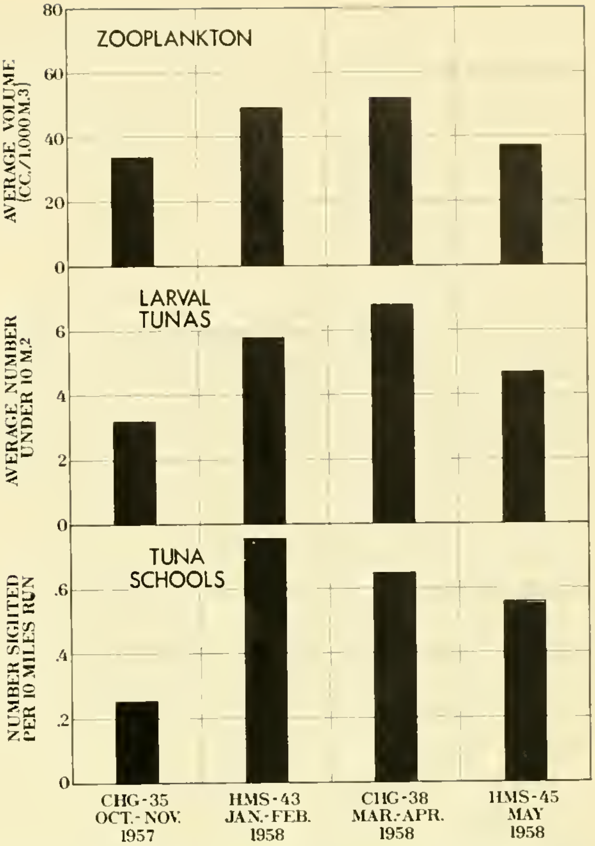

FIGURE 5.—Average abundance of zooplankton, larval tunas, and tuna schools for the offshore surveys.

ABUNDANCE OF LARVAL AND ADULT TUNAS

Strasburg (1960) found a tendency for larval tunas to occur in larger abundance where there were more adults of the same species although the correlation was statistically nonsignificant. Similar comparisons by species were not possible with our data. Schools of adult tunas were located by sighting the associated bird flocks. Because of the necessity of covering a certain distance of the offshore surveys

TABLE 6.—*Average number of larval tunas under 10 m.² of ocean surface and number of schools sighted per 10-mile run for the legs of the offshore surveys*

Cruise	North leg		East leg		South leg		West leg		Entire survey	
	Schools	Larvae	Schools	Larvae	Schools	Larvae	Schools	Larvae	Schools	Larvae
CHG-35	0.405	3.2	0.183	1.8	0.207	3.4	0.226	4.3	0.256	3.2
HMS-43	1.020	7.2	.884	5.4	.569	6.8	.560	3.6	.758	5.8
CHG-38	.909	14.6	.390	4.4	.591	4.3	.708	3.9	.649	6.8
HMS-45	.591	3.9	.275	9.4	1.013	2.9	.380	2.9	.559	4.7

within an allotted time, investigation of schools was discontinued if the response to chumming was unfavorable. Consequently, the specific identity of many of the schools was not determined, and our examination of the relation between larval and adult abundance was in terms of the aggregate of all tuna species.

In comparing the number of schools sighted per 10-mile run and the average number of larval tunas under 10 m.² of ocean surface for the legs of the offshore surveys and for the inner, middle, and outer 75-mile sections of these legs, no significant correlations (Spearman rank correlation) were found (tables 6 and 7). For the entire offshore survey area, the averages for both adult tuna schools and larval tunas were highest during either HMS-43 or CHG-38, slightly lower during HMS-45, and lowest during CHG-35. A similar pattern was found in the average of zooplankton volumes. The variations of all three averages are illustrated in figure 5.

TABLE 7.—*Average number of larval tunas under 10 m.² of ocean surface and number of schools sighted per 10-mile run for 75-mile sections of the legs of the offshore surveys*

Cruise	Inner 75 miles		Middle 75 miles		Outer 75 miles	
	Schools	Larvae	Schools	Larvae	Schools	Larvae
CHG-35	0.452	2.8	0.305	3.0	0.030	3.7
HMS-43	.867	3.0	.554	7.4	.833	7.3
CHG-38	1.145	6.8	.460	7.1	.393	6.5
HMS-45	.412	3.8	.586	6.0	.695	3.9

INFERENCES CONCERNING SKIPJACK SPAWNING

Inferences about spawning based on the size of the larva upon hatching have been discussed by Matsumoto (1958). He hypothesized that skipjack are 2.5 mm. or less at hatching, that the eggs and larvae are planktonic and therefore subject to dispersion by currents, but that their displacement from the spawning site would be relatively insignificant unless the currents were exceptionally strong. Larval skipjack have been taken throughout the area around the Marquesas Islands (fig. 4). Most of the catch consisted of larvae between 3 and 4.5 mm. long, so we may assume that they had hatched recently. Since the currents around the Marquesas Islands are suspected to be weak (Sverdrup, Johnson, and Fleming, 1942: p. 702), these larvae could not have drifted very far from the spawning sites. Thus, skipjack spawning appears to occur throughout the sampled area.

Matsumoto (1958) has reported larval skipjack catches from long. 180° to 120° W., and on the basis of records of larvae and juveniles taken in the Philippine Islands (Wade, 1951) and off the coast of Central America (Schaefer and Marr, 1948; Mead, 1951) and of juveniles caught in the Marshall Islands (Marr, 1948), he has indicated the possibility that skipjack spawn throughout the equatorial waters of the Pacific. Subsequently, Klawe (1963) noted the occurrence of larval skipjack in the eastern tropical Pacific. Matsumoto (unpublished) recently obtained larval skipjack from areas west of 180°, particularly around the Marshall Islands and the eastern part of the Caroline Islands. Capture of larval skipjack in localities still farther west in the Marianas and Palau Islands was reported by Yabe, Yabuta, and Ueyanagi (1963). These records confirm Matsumoto's hypothesis of the transoceanic distribution of larval skipjack in the Pacific.

Matsumoto (1958) also has reported the north-south distribution of larval skipjack as extending from lat. 25° N., to 14½° S. in the central Pacific. The southern limit now may be extended to at least lat. 18° S.

Table 8 shows the months during which larval skipjack have been taken in northeastern French Oceania on various cruises by vessels of the Bureau of Commercial Fisheries. They were captured in all months except July, in which no sampling was done. Thus, skipjack spawning can be inferred to occur throughout the year in these waters. Yoshida (1965) likewise concluded from a study of skipjack ovaries that skipjack spawn year-round in the Marquesas.

Yoshida also concluded that spawning is greatest from November through April. Although the seasonal distribution of larval skipjack (fig. 3) is consistent with Yoshida's results, the data do not permit a comparison for all seasons.

Table 8.—*Months, years, and cruises during which larval skipjack have been captured in northeastern French Oceania. Italicized cruises sampled the Marquesan offshore survey area.*

[Data prior to October 1957 from Matsumoto (1958) and Strasburg (1960)]

Month	Year			
	1952	1956	1957	1958
January	----------	----------	----------	*HMS-43*
February	----------	----------	HMS-38 *CHG-32*	*HMS-43*
March	----------	HMS-33	HMS-38 *CHG-32*	*CHG-38*
April	----------	----------	----------	*CHG-38*
May	----------	----------	----------	*HMS-45*
June	*HMS-15*	----------	----------	*HMS-45*
July				
August	----------	CHG-30	----------	----------
September	----------	*CHG-30*	----------	----------
October	----------	----------	*CHG-35*	----------
November	HMS-18	----------	*CHG-35*	----------
December	----------	----------	*CHG-35*	----------

SUMMARY

1. The results of a study of the distribution of larval tunas in Marquesan waters are presented. Data were collected in 1957 and 1958 on repeated transits of a standardized offshore survey pattern and on repeated visits to a single station where diel variability of larval abundance was studied.

2. Larval tunas were sorted and counted from 113 plankton samples from the offshore surveys and 92 from the diel variability station. Larval abundance is expressed as the number of larvae under 10 m.^{2} of ocean surface down to a depth of 140 m.

3. Duplicability of larval catches by oblique tows taken at night or day was demonstrated.

4. Greater abundance of larval skipjack during darkness was evident at the diel variability station in December 1957 and March 1958 and of larval yellowfin in January 1958. Greater abundance of larval skipjack at twilight was found in April and June of 1958. Results of attempts to determine whether larvae were below 140 m. were inconclusive.

5. Data from the offshore surveys indicate greater abundance of larval tunas during the Marquesan summer and fall (January to April) than during other months.

6. Larval skipjack have been collected throughout the area of northeastern French Oceania bounded by long. 130° W. and 147° W. from the Equator to lat. 18° S.

7. High and low catches of larvae occurred in samples of high as well as of low plankton volume.

8. Average abundances of zooplankton, larval tunas, and tuna schools for the offshore surveys were lowest during CHG–35 (Oct.–Nov. 1957), highest during either HMS–43 (Jan.–Feb. 1958) or CHG–38 (Mar.–Apr. 1958), and intermediate during HMS–45 (May 1958).

9. According to records of the localities of the capture of larvae and juveniles, skipjack spawn throughout the tropical and subtropical zones of the Pacific Ocean. In northeastern French Oceania, skipjack appear to spawn throughout the year. The data are consistent with the conclusion reached from a study of skipjack ovaries that the spawning of skipjack in northeastern French Oceania is most active from November through April.

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APPENDIX

Table A–1.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Charles H. Gilbert *cruise 35*

Station	Date (1957)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
18	Oct. 21	0739–0811	0–140	2185.1	5	-----	-----	-----	-----	-----	-----	5
19	do	0814–0845	0–140	2112.5	4	-----	-----	-----	-----	-----	1	5
20	do	1035–1105	0–140	1927.0	2	-----	-----	1(?)	-----	-----	3	6
21	do	1108–1137	0–140	1895.9	13	-----	4(?)	-----	-----	-----	-----	17
22	do	1335–1405	0–140	1789.0	-----	-----	-----	-----	-----	-----	-----	0
23	do	1406–1434	0–140	1860.8	-----	-----	-----	-----	-----	-----	-----	0
24	do	1632–1703	0–140	2082.5	-----	-----	-----	-----	-----	-----	-----	0
25	do	1706–1737	0–140	2068.2	1	-----	-----	-----	-----	-----	-----	1
26	do	1933–2005	0–140	2331.2	5	1	-----	-----	-----	-----	4	10
27	do	2007–2037	0–140	1842.2	11	-----	-----	-----	-----	-----	-----	11
28	do	2235–2305	0–140	1735.6	5	-----	-----	-----	-----	-----	-----	5
29	do	2306–2338	0–143	1979.1	9	-----	1	-----	-----	-----	-----	10
30	Oct. 22	0143–0213	0–140	2039.6	2	-----	-----	-----	-----	-----	1	3
31	do	0214–0244	0–140	2078.5	2	1	-----	-----	-----	-----	-----	3
32	do	0431–0459	0–140	1733.9	5	1	-----	-----	-----	-----	-----	6
33	do	0501–0532	0–140	2073.1	7	-----	-----	-----	-----	-----	-----	7
119	Dec. 1	0608–0638	0–140	1705.9	17	-----	-----	-----	-----	-----	-----	17
120	do	0639–0711	0–143	1936.4	6	-----	-----	-----	-----	-----	-----	6
121	do	0905–0936	0–140	1709.6	11	-----	-----	-----	-----	-----	1	12
122	do	0939–1008	0–140	1917.3	19	-----	-----	-----	-----	1	-----	20
123	do	1205–1237	0–140	1681.6	6	-----	-----	-----	-----	-----	-----	6
124	do	1239–1310	0–140	1599.5	6	-----	-----	-----	-----	2	2	10
125	do	1506–1537	0–142	1765.8	6	-----	1	-----	-----	-----	-----	7
126	do	1539–16 0	0–142	1809.0	6	-----	-----	-----	1	-----	2	9
127	do	1805–1835	0–140	1361.9	5	-----	-----	-----	-----	-----	-----	5
128	do	1836–1907	0–140	1352.2	7	-----	-----	-----	-----	-----	-----	7
129	do	2103–2133	0–140	1375.9	12	-----	-----	-----	-----	1	1	14
130	do	2134–2006	0–140	1503.4	11	-----	1	-----	-----	5	-----	17
131	Dec. 2	0005–0035	0–140	1481.8	14	-----	2	1(?)	-----	13	-----	30
132	do	0037–0106	0–140	1516.9	18	-----	2(?)	1(?)	1	23	4	49
133	do	0304–0334	0–140	1564.6	26	-----	-----	-----	-----	30	-----	56
134[2]	do	0336–0405	0–140	1649.7	8	-----	-----	-----	-----	-----	-----	8

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[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

[2] Sample considered atypical because salps comprised 95 percent (estimated) of the volume and 71 percent (estimated) of the organisms.

Table A–2.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Hugh M. Smith *cruise 43*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
22–1	Jan. 23	1622–1655	0–145	1991.9	2	5	-----	-----	-----	-----	-----	7
22–2	do	1825–1855	0–145	2023.7	3	1	-----	-----	-----	-----	-----	4
22–3	do	2005–2040	0–158	2104.9	-----	2	2	-----	-----	-----	-----	4
22–4	do	2207–2238	0–140	1711.4	4	11	5	-----	-----	-----	-----	20
22–5	Jan. 24	0013–0048	0–140	2223.4	-----	11	4	-----	-----	1	-----	16
22–6	do	0210–0241	0–141	1887.6	2	13	4	-----	-----	-----	1	20
22–7	do	0408–0438	0–148	1787.0	1	4	2	-----	-----	-----	-----	7
22–8	do	0615–0649	0–158	1716.8	-----	1	-----	-----	-----	-----	-----	1
22–9	do	0803–0832	0–140	1528.0	-----	-----	-----	-----	-----	-----	-----	0
22–10	do	1012–1042	0–149	1568.6	-----	1	1	-----	-----	-----	-----	2
22–11	do	1208–1245	0–158	1986.8	-----	-----	-----	-----	-----	-----	-----	0
22–12	do	1401–1431	0–140	1559.6	2	5	-----	-----	-----	-----	1	8

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[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A-3.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Charles H. Gilbert *cruise 38*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	$M.^3$	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
34-A	Mar. 6	0806-0836	0-140	1885. 5	3	----	----	----	----	----	----	3
34 B	do	1003-1033	0-141	1476. 7	----	----	----	----	----	1	----	1
34 C	do	1205-1237	0-140	1896. 6	3	----	----	----	----	----	----	3
34-D	do	1408-1438	0-140	1938. 8	1	----	----	----	----	----	----	1
34-E	do	1608-1636	0-140	1486. 8	1	----	----	----	----	----	----	1
34-F	do	1807-1837	0-142	1949. 7	----	1	----	----	----	----	----	1
34-G	do	2006-2036	0-142	1902. 2	4	----	----	----	----	1	----	5
34-H	do	2210-2240	0-140	1624. 9	10	1	----	----	----	----	----	11
34-I	Mar. 7	0006-0037	0-142	1737. 6	5	----	----	----	----	1	----	6
34-J	do	0205-0235	0-140	1907. 0	8	----	----	----	----	1	----	9
34-K	do	0403-0434	0-142	1884. 9	14	----	----	----	----	----	----	14
34-L	do	0604-0634	0-140	1703. 9	8	3	----	----	----	----	----	11
93-A	Apr. 17	1311-1341	0-140	1608. 2	----	----	----	----	----	----	----	0
93-B	do	1503-1533	0-140	1629. 9	----	----	----	----	----	----	----	0
93-C	do	1702-1732	0-140	1512. 7	----	----	----	----	----	----	----	0
93-D	do	1903-1933	0-142	1847. 0	4	----	----	----	----	----	----	4
93-E	do	2102-2132	0-140	1630. 8	----	----	----	----	----	----	----	0
93-F	do	2306-2336	0-140	1719. 8	2	----	----	----	----	----	----	2
93-G	Apr. 18	0102-0133	0-142	1697. 4	2	----	----	----	----	----	----	2
93-H	do	0302-0332	0-142	1668. 4	1	----	1	----	----	----	----	2
93-I	do	0503-0533	[2]?	1478. 7	3	----	----	----	----	----	----	3
93-J	do	0702-0732	0-140	1478. 4	3	----	----	----	----	----	----	3
93-K	do	0903-0934	0-142	1696. 3	2	----	----	----	----	----	----	2
93 L	do	1102-1132	0-140	1573. 3	2	----	----	----	----	----	----	2

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

[2] Cable meter failed.

TABLE A-4.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Hugh M. Smith *cruise 45*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	$M.^3$	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
120-1	June 8	1522-1552	0-122	937. 5	1	----	----	----	----	----	----	1
120-2	do	1522-1552	112-230	606. 7	----	----	----	----	----	----	----	0
121-1	do	1710-1739	0-125	797. 5	3	----	----	----	----	----	----	3
121-2	do	1710-1739	96-239	445. 0	----	----	----	----	----	----	----	0
122-1	do	1914-1941	0-126	845. 2	3	----	----	----	----	----	----	3
122-2	do	1914-1941	112-238	1041. 1	----	----	----	----	----	----	----	0
123-1	do	2105-2133	0-126	941. 4	----	----	----	----	----	----	----	0
123-2	do	2105-2133	71-238	1003. 0	----	----	----	----	----	----	----	0
124-1	do	2313-2347	0-137	865. 6	[2]1	----	----	----	----	----	----	1
124-2	do	2313-2347	103-240	394. 6	----	----	----	----	----	----	----	0
125-1	June 9	0110-0144	0-137	852. 6	----	1	----	----	----	----	----	1
125-2	do	0110-[3]?	70-240	1482. 7	----	----	----	----	----	----	----	0
126-1	do	0308-0335	0-121	794. 0	----	----	----	----	----	----	----	0
126-2	do	0308-0335	107-229	598. 8	----	----	----	----	----	----	----	0
127-1	do	0510-0539	0-126	817. 8	4	----	----	----	----	----	----	4
127-2	do	0510-0539	103-238	681. 1	----	----	----	----	----	----	----	0
128-1	do	0711-0737	0-125	794. 3	----	----	----	----	----	----	----	0
128-2	do	0711-0737	94-245	447. 1	----	----	----	----	----	----	----	0
129-1	do	0910-0937	0-126	718. 5	----	----	----	----	----	----	----	0
129-2	do	0910-0937	76-238	939. 8	----	----	----	----	----	----	----	0
130-1	do	1108-1149	0-150	855. 4	----	----	----	----	----	----	----	0
130-2	do	1108-1149	71-262	[4]471. 3	----	----	----	----	----	----	----	0
131-1	do	1306-1333	0-123	702. 0	----	----	----	----	----	----	----	0
131-2	do	1306-1333	116-239	920. 6	----	----	----	----	----	----	----	0

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna

[2] A 27-mm. juvenile.

[3] Messenger time was not recorded.

[4] Flowmeter recording was extremely low.

TABLE A-5.—*Data on larval tunas collected during the offshore survey on* Charles H. Gilbert *cruise 35*

Station	Position		Date (1957)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
35	9°16′	137°52′	Oct. 24	2301–2329	0–182	1681. 0	------	------	------	------	------	------	------	0
36	9°16′	137°52′	do	2333–0001	0–140	1546. 8	------	------	------	------	------	------	------	0
38	9°22′	137°30′	Oct. 25	0259–0330	0–140	1316. 0	------	------	------	------	------	------	------	0
38A	9°22′	137°30′	do	0332–0401	0–140	1487. 2	------	------	------	------	------	------	------	0
38B	9°14′	136°20′	do	2256–2327	0–140	1760. 4	2	1	------	------	------	------	------	3
39	9°14′	136°20′	do	2329–0001	0–140	1797. 9	4	1	3	------	------	------	------	8
41	9°14′	136°34′	Oct. 26	0258–0329	0–173	1750. 1	5	------	------	------	------	------	3	8
42	9°14′	136°34′	do	0330–0401	0–140	1694. 2	2	------	------	------	------	------	5	7
44	9°17′	139°02′	do	2259–2329	0–140	1486. 1	------	------	------	------	------	------	------	0
45	9°17′	139°02′	do	2331–0003	0–140	1582. 7	[2]1	------	------	------	------	------	------	1
47	9°17′	139°16′	Oct. 27	0254–0324	0–140	1558. 2	------	------	------	------	------	------	------	0
48	9°17′	139°16′	do	0326–0357	0–140	1463. 9	------	------	------	------	------	------	------	0
50	11°03′	139°33′	do	2300–2330	0–140	1530. 1	4	------	------	------	------	------	1	5
51	11°03′	139°33′	do	2332–0000	0–140	1354. 9	2	------	------	------	------	------	------	2
53	11°22′	139°27′	Oct. 28	0258–0328	0–140	1533. 9	5	------	------	------	------	------	------	5
54	11°22′	139°27′	do	0330–0401	0–140	1655. 9	7	------	------	------	------	------	1	8
55	12°23′	139°36′	do	2300–2331	0–140	2011. 0	------	------	------	------	------	------	------	0
56	12°23′	139°36′	do	2332–0000	0–140	1722. 6	6	------	------	------	------	------	------	6
58	12°09′	139°30′	Oct. 29	0258–0327	0–140	1527. 4	5	------	------	------	------	------	------	5
59	12°09′	139°30′	do	0329–0358	0–140	1453. 1	6	------	------	------	------	------	------	6
60	9°36′	139°44′	Oct. 30	0300–0328	0–140	1134. 0	------	------	------	------	------	------	------	0
61	9°36′	139°44′	do	0329–0400	0–140	1336. 5	1	------	------	------	------	------	------	1
62A	7°20′	139°32′	Nov. 1	2258–2329	0–140	1663. 2	6	------	------	------	------	------	------	6
63	7°20′	139°32′	do	2331–2359	0–140	1414. 5	2	------	------	------	------	------	------	2
65	7°06′	139°30′	Nov. 2	0257–0327	0–140	3365. 6	------	------	------	------	------	------	------	0
66	7°06′	139°30′	do	0332–0400	0–140	1633. 8	------	------	------	------	------	------	------	0
67	6°04′	139°50′	do	2257–2327	0–140	1788. 8	------	------	------	------	------	------	------	0
68	6°04′	139°50′	do	2329–0000	0–140	1915. 1	2	1	------	------	------	------	1	4
70	6°26′	139°52′	Nov. 3	0302–0333	0–140	1807. 4	------	------	------	------	------	------	------	0
71	6°26′	139°52′	do	0349–0419	0–140	1755. 8	6	------	------	------	------	------	------	6
73	8°36′	139°31′	do	2305–2334	0–140	1390. 0	8	------	------	------	------	------	------	8
74	8°36′	139°31′	do	2335–0005	0–140	1408. 0	5	------	------	------	------	2	------	7
76	8°54′	139°38′	Nov. 4	0300–0330	0–140	854. 4	2	------	------	------	------	3	------	5
77	8°54′	139°38′	do	0334–0404	0–140	715. 8	------	------	------	------	------	------	------	0
79	9°13′	141°35′	do	2258–2328	0–140	2218. 6	14	------	------	1	------	------	2	17
80	9°13′	141°35′	do	2331–0002	0–140	2168. 1	14	1	------	------	------	------	------	15
82	9°12′	142°00′	Nov. 5	0256–0326	0–140	1813. 9	1	------	------	------	------	------	------	1
83	9°12′	142°00′	do	0328–0356	0–140	1786. 6	1	------	------	------	------	------	------	1
84	9°15′	142°46′	do	2259–2329	0–140	1490. 9	------	------	------	------	------	------	------	0
85	9°15′	142°46′	do	2332–0004	0–140	1580. 6	------	------	------	------	------	------	------	0
87	9°18′	142°23′	Nov. 6	0258–0329	0–140	1496. 6	3	------	------	------	------	------	1	4
88	9°18′	142°23′	do	0334–0403	0–140	1449. 6	12	------	------	------	------	------	------	12
90	9°15′	140°33′	do	2256–2326	0–140	1267. 4	1	------	------	------	------	------	------	1
91	9°15′	140°33′	do	2328–2358	0–140	1192. 9	------	------	------	------	------	------	------	0
93	9°13′	140°10′	Nov. 7	0258–0328	0–140	1264. 4	4	------	------	------	------	------	1	5
94	9°13′	140°10′	do	0332–0402	0–140	1074. 6	6	------	------	------	------	------	------	6

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

[2] A juvenile about 25 mm. long.

TABLE A-6.—*Data on larval tunas collected during the offshore survey on* Hugh M. Smith *cruise 43*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
30	9°12′	139°17′	Jan. 27	2116–2151	0–141	1755. 7	------	------	------	------	------	------	------	0
32	9°12′	138°48′	Jan. 28	0313–0342	0–160	1300. 0	2	------	2	------	------	------	1	5
34	9°10′	136°50′	do	2110–2140	0–147	1750. 6	13	1	------	------	------	------	------	14
36	9°10′	136°18′	Jan. 29	0313–0343	0–145	1617. 9	6	------	------	------	------	------	------	6
39	9°37′	139°40′	Jan. 30	2109–2139	0–148	1688. 4	------	------	------	------	------	------	------	0
41	10°14′	139°38′	Jan. 31	0312–0342	0–148	1516. 8	3	------	------	------	------	------	------	3
42	12°02′	139°36′	do	2112–2142	0–154	1466. 3	10	------	------	------	------	------	------	10
44	12°31′	139°34′	Feb. 1	0313–0343	0–185	1158. 6	3	------	------	------	------	------	------	3
47	11°16′	139°42′	do	2110–2141	0–141	1551. 1	12	3	------	------	------	------	2	17
49	10°43′	139°39′	Feb. 2	0313–0343	0–141	582. 7	3	------	1	------	------	------	------	4
57	9°07′	141°05′	Feb. 5	2118–2145	0–141	1264. 6	------	------	------	------	------	------	------	0
59	9°08′	141°32′	Feb. 6	0319–0344	0–142	1384 6	------	------	------	------	------	------	------	0
60	9°13′	143°02′	do	2113–2143	0–140	1403. 1	13	------	------	------	------	------	------	13
62	9°15′	142°26′	Feb. 7	0315–1337	0–145	1468. 9	6	------	------	------	------	------	------	6
64	9°13′	140°41′	do	2109–2133	0–167	1039. 8	2	------	------	------	------	------	------	2
66	9°16′	140°06′	Feb. 8	0318–0348	0–140	1511. 9	------	------	------	------	------	------	------	0
70	7°35′	139°40′	Feb. 9	2110 2137	0–140	1164. 9	13	1	------	------	------	------	------	14
71	6°52′	139°40′	Feb. 10	0330–0359	0–141	1386. 1	3	------	------	------	------	------	------	3
73	5°37′	139°50′	do	2113–2142	0–140	1363. 7	8	1	------	------	------	------	------	9
75	6°21′	139°38′	Feb. 11	0319–0347	0–141	1279. 6	1	------	------	------	------	------	------	1
76	8°30′	139°40′	do	2120–2146	0–140	957. 7	1	------	------	------	------	------	------	1
78	9°03′	139°45′	Feb. 12	0312–0341	0–140	1199. 9	5	1	------	------	------	4	------	10

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A-7.—*Data on larval tunas collected during the offshore survey on* Charles H. Gilbert *cruise 38*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
46	9°11′	138°06′	Mar. 26	2204-2234	0-140	1416.2	----	----	----	----	----	----	----	0
48	9°09′	137°34′	Mar. 27	0405-0435	0-142	1647.2	1	----	----	----	----	----	----	1
49	9°11′	136°15′	do	2104-2135	0-142	1703.6	5	----	----	----	----	----	----	5
51	9°07′	136°56′	Mar. 28	0304-0334	0-140	1776.7	6	----	----	----	----	----	----	6
53	9°09′	138°53′	do	2122-2151	0-140	1394.2	----	----	----	----	----	----	----	0
55	9°08′	139°27′	Mar. 29	0303-0332	0-140	1338.6	14	2	----	----	----	----	----	16
57	7°32′	139°46′	do	2104-2134	0-142	1275.6	29	----	10	----	----	----	----	39
59	6°57′	139°44′	Mar. 30	0305-0336	0-142	1363.8	2	----	----	----	----	----	----	2
60	5°44′	139°40′	do	2102-2132	0-140	1644.4	4	----	----	----	----	----	----	4
62	6°20′	139°39′	Mar. 31	0307-0337	0-140	1505.8	12	----	5	1	----	----	----	18
64	8°10′	139°44′	do	2103-2133	0-142	1475.9	13	2	1	----	----	----	----	16
66	8°38′	139°57′	Apr. 1	0306-0336	0-142	1456.4	8	----	----	----	----	----	----	8
69	9°08′	141°14′	Apr. 3	2104-2134	0-140	1543.7	1	----	----	----	----	----	----	1
71	9°07′	141°52′	Apr. 4	0309-0339	0-140	1751.3	6	----	----	----	----	----	----	6
72	9°05′	142°58′	do	2102-2133	0-142	1885.5	9	----	----	----	----	----	----	9
74	9°04′	142°28′	Apr. 5	0304-0334	0-142	1657.8	3	----	----	----	----	----	----	3
75	9°09′	140°28′	do	2103-2132	0-140	1212.8	----	----	----	----	----	----	----	0
77	9°12′	139°57′	Apr. 6	0309-0339	0-140	1333.3	8	----	----	----	----	----	----	8
78	10°52′	139°45′	do	2107-2137	0-142	1407.8	----	----	----	----	----	----	----	0
80	11°28′	139°48′	Apr. 7	0304-0335	0-140	1627.7	6	----	----	----	----	----	----	6
81	12°32′	139°43′	do	2103-2133	0-140	1546.5	5	1	----	----	----	----	----	6
83	12°00′	139°41′	Apr. 8	0305-0335	0-140	1921.8	12	----	----	----	----	----	----	12
84	10°02′	139°44′	do	2100-2130	0-142	1406.7	1	----	----	----	----	----	----	1
86	9°24′	139°51′	Apr. 9	0302-0332	0-142	1536.7	6	----	----	----	----	----	----	6

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A-8.—*Data on larval tunas collected during the offshore survey on* Hugh M. Smith *cruise 45*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*^{3}	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
78	9°08′	138°10′	May 15	2004-2030	0-140	1392.8	4	----	----	----	----	----	----	4
79	9°12′	137°22′	May 16	0317-0346	0-161	1611.1	34	----	----	----	----	----	----	34
82	9°10′	136°10′	do	2000-2028	0-140	1432.8	6	2	----	----	----	----	----	8
83	9°13′	137°02′	May 17	0320-0347	0-139	1321.9	2	----	----	----	----	----	----	2
84	9°12′	139°07′	do	1959-2029	0-125	1601.3	3	----	1	----	----	----	----	4
87	9°12′	141°22′	May 19	2000-2029	0-140	1578.1	----	----	----	----	----	----	----	0
88	9°12′	142°02′	May 20	0313-0343	0-137	1357.3	----	----	----	----	----	----	----	0
90	9°12′	143°08′	do	1955-2026	0-140	1536.0	----	----	2	1	----	----	----	3
91	9°14′	142°20′	May 21	0309-0338	0-140	1592.1	4	----	3	5	----	----	----	12
94	9°12′	140°36′	do	2002-2031	0-137	1359.1	1	----	----	----	----	----	----	1
97	7°39′	139°45′	May 23	2001-2030	0-140	1421.6	1	----	9	----	----	----	----	10
98	6°54′	139°41′	May 24	0314-0343	0-140	1426.5	----	----	----	----	----	----	----	0
101	5°38′	139°40′	do	1958-2028	0-138	1491.0	2	----	3	----	----	----	1	6
102	6°24′	139°38′	May 25	0310-0344	0-140	1759.2	2	1	----	----	----	----	----	3
105	8°25′	139°42′	do	1959-2034	0-137	1926.3	2	----	----	----	----	----	----	2
107	10°55′	139°40′	May 27	2000-2028	0-139	1301.2	4	----	----	----	----	----	----	4
108	11°30′	139°39′	May 28	0312-0339	0-144	2165.0	----	----	----	----	----	----	----	0
110	12°41′	139°39′	do	2001-2040	0-133	2347.5	----	----	----	----	----	----	----	0
111	11°58′	139°40′	May 29	0306-0336	0-124	1459.1	----	----	----	----	----	----	----	0
113	10°11′	139°34′	do	1953-2025	0-140	1928.4	15	----	1	----	----	----	----	16
114	9°25′	139°34′	May 30	0315-0351	0-146	944.9	----	----	----	----	----	1	----	1

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

ASSOCIATION OF FISHES WITH FLOTSAM IN THE OFFSHORE WATERS OF CENTRAL AMERICA

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ABSTRACT

During April, May, June, and October, 1963, a total of 70 purse seine collections were made of the fishes associated with floating objects. Nearly all of these collections were from the offshore waters of Costa Rica. Twelve families of fishes (Lobotidae, Carangidae, Coryphaenidae, Mullidae, Kyphosidae, Pomacentridae, Scombridae, Blenniidae, Stromateidae, Mugilidae, Polynemidae, and Balistidae) and 32 species were represented in the collections. Most of the species were present during both spring and fall, and nearly all of the fishes were juveniles.

Nine of the 32 species, including the 2 most abundant ones, *Caranx caballus* Günther and *Selar crumenophthalmus* (Bloch), were carangids. The lengths of two species, *Abudefduf saxatilis* (Linnaeus) and *Seriola* sp. were greater the farther an object was located from shore. Some species such as *C. caballus*, *Psenes pacificus* Meek and Hildebrand, and *Canthidermis maculatus* (Bloch) were present in almost a complete series of juvenile stages; others as *Chromis atrilobata* Gill, *Pseudupeneus grandisquamis* (Gill), and *Agonostomus monticola* (Bancroft) were represented by only a single juvenile stage. More fishes were collected under large objects than under small objects. The total number of individuals present near moored objects after 5 days did not differ from the numbers present after 20 or more days. The coloration of fishes was related to their association behavior. Silvery colored fishes did not remain as close to the object as did the more darkly colored species. Most adult fishes, which did not remain as near the object as did juveniles, appeared beneath an object only intermittently. *Canthidermis maculatus*, however, maintained close contact with drifting objects both as adults and juveniles.

Observations of the behavior of species are discussed in relation to the mechanisms for the association of fish with flotsam that have been postulated by other authors. None of their hypotheses was supported by our data. Additional mechanisms were postulated.

The association of fishes with floating objects has been exploited by a number of fisheries. Japanese pole-and-line fisheries and American purse seine and live-bait fisheries take advantage of the association of yellowfin tuna, *Thunnus albacares* (Bonnaterre), and oceanic skipjack, *Katsuwonus pelamis* (Linnaeus), with algae, logs, and other flotsam (Uda, 1933; McNeely, 1961). Uda and Tsukushi (1934), and Yabe and Mori (1950) reported that log-associated schools of tuna provide a consistently higher yield per unit fishing effort than unassociated schools.

Moored rafts of bamboo or palm fronds are used to attract dolphin-fish, *Coryphaena hippurus* (Linnaeus), in seine fisheries of Japan (Kojima, 1955, 1956, 1960a, 1960b, and 1961). Moored cork-slabs serve the same purpose for Maltese fishermen (Galea, 1961). Two types of palm-frond rafts are used by Indonesian fishermen to attract various clupeids, scombrids, *Decapterus* spp., and other carangids (Hardenberg, 1950; Soemarto, 1960). In addition to these commercially important species, many others of lesser or no commercial value are also encountered (Murray and Hjort (1912), Yabe and Mori (1950), Uchida and Shojima (1958), Besednov (1960), Kojima (1960a), Mansueti (1963), and Gooding and Magnuson[1]).

Note: Approved for publication March 8, 1966.

[1] Reginald M. Gooding and John J. Magnuson—Observations on the ecology and behavior of fishes around a drifting raft near Hawaii during the first 48 hours adrift. Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

Gooding and Magnuson reviewed the hypotheses that have been advanced to explain this habit: (1) attraction by food (smaller fish, algae, decaying palm fronds, and plankton made more visible by the shade of the object); (2) negative phototaxis in response to the shadow cast by the object; (3) shelter from predators; and (4) use of the object as a spawning substrate. They also suggested an additional hypothesis that floating objects are cleaning stations where pelagic fishes go to have their parasites removed by other fish.

This paper provides information on the ecology and behavior of fishes associated with floating objects in the offshore waters of Central America. Special attention is given to the frequency, abundance, and size of the species which compose flotsam-associated aggregations and how these characteristics are related to the location and size of the object. These studies are the framework upon which future behavior investigations will be based. The aim of our program is to determine whether a device can be designed that will be maximally efficient in aggregating tuna and skipjack. The potential value to the tuna fishery of establishing such devices has been discussed by Alverson and Wilimovsky (1963).

PROCEDURES

Nearly all of our studies were in the offshore waters of Costa Rica (fig. 1) because yellowfin tuna and skipjack are often associated with the flotsam in this region (logbook records obtained through the courtesy of the Inter-American Tropical Tuna Commission). Several collections were near the coast of southern Mexico and 1 near Cocos Island. Samples were collected by encircling flotsam and its associated fauna with a small 7/16-inch (11 mm.) stretch-mesh purse seine, 12 feet deep (3.7 m.) and 110 feet (33.5 m.) long (Aasted, MS.)[2]. An average of 66 percent of the fishes observed beneath an object were captured in the seine. Fish larger than 100 mm. standard length may have escaped the net, and fish smaller than 15 mm. occasionally swam through the webbing. When the net was set, fish tended to stay near the flotsam or even swim upward. Thus, fish swimming at a depth greater than the maximum depth of the seine also may have been caught. Sampling errors due to fish escaping from or entering the seined cylinder of water were probably small.

Twenty-three purse seine collections of fishes were made during April, May, and June, 1963, and 47 during October. Of these samples, 62 were of fishes associated with naturally occurring flotsam, and 8 were of fishes collected beneath moored logs, buoys, and other objects.

After a collection was made, the success of the set was estimated, the object was described and measured, and motile and attached organisms were preserved. In the October studies, to determine the rate and direction of movement of drifting materials, all objects were tagged and marked with a small flag prior to release. Underwater observations and cinematic photographs were used to describe the behavior and estimate the abundance of fishes.

CHARACTERISTICS AND DISTRIBUTION OF FLOTSAM

Far more drifting materials were in the study area in October than in the spring. The Gulf of Nicoya was littered with floating logs and other plant debris. The greater abundance of flotsam in October was not surprising because rainfalls are usually heaviest during this period (Peterson, 1960).

Fish were not seen beneath the flotsam in the Gulf and were only rarely associated with inshore logs between Cape Blanco and Piedra Blanca (fig. 1). Northwest of this area, however, nearly every drifting object encountered had its own associated fish population. Most often these objects were aggregated in areas of current convergence.

During April, May, and June, currents in the area usually set northwest at an estimated 2 knots; currents also set northwest during October but were not as strong. Three logs tagged in October and later recovered had drifted northwest at 0.28, 0.45, and 0.33 knot.

Only one of the drifting objects sampled had attached invertebrates—goose barnacles, *Conchoderma virgatum* (Spengler). This species and other goose barnacles of the genus *Lepas* were found in quantity on moored objects after 14 or more days.

Adult and megalops grapsoid crabs of the genus *Plagusia* were numerous on nearly all logs. Individuals in the megalops stage frequently were swimming near drifting objects.

SEASONAL VARIATION IN OCCURRENCE OF FISH

Over 12,000 fishes were captured beneath floating objects in this study; 12 families and 32 species were

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[2] Donald C. Aasted. A miniature purse seine for capturing small pelagic fishes. Manuscript, Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, Calif.

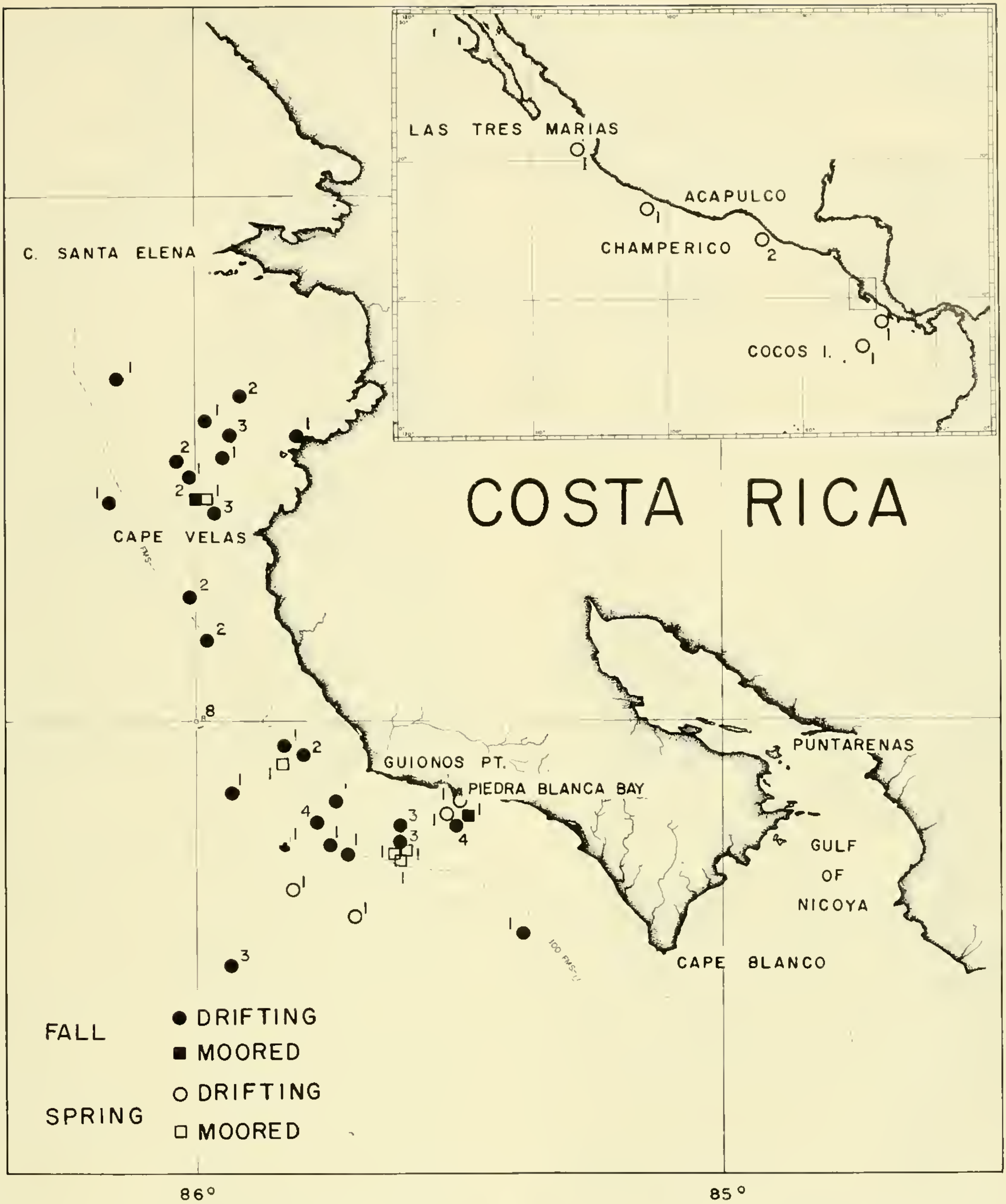
LAS TRES MARIAS
ACAPULCO
CHAMPERICO
COCOS I.
11°
C. SANTA ELENA
COSTA RICA
CAPE VELAS
10°
GUIONOS PT.
PIEDRA BLANCA BAY
PUNTARENAS
GULF OF NICOYA
CAPE BLANCO
FALL
● DRIFTING
■ MOORED
SPRING
○ DRIFTING
□ MOORED
86°
85°

FIGURE 1.—Positions of collections made of fishes beneath flotsam in April, May, and June 1963 (spring) and October 1963 (fall). Numerals indicate number of collections made in each locality. Inset at top shows location of study area and position of the six collections made outside this area.

represented. The scientific name, family, and season of occurrence of these species are presented in table 1. Abbreviated names are used in the text and subsequent tables.

There was little seasonal variation in the occurrence of species. Twenty-four of the total of 32 species were captured or observed during both spring and fall. The seasonal occurrence of adult

Table 1.—*Length, life stage, and seasonal occurrence of species collected beneath flotsam in the offshore waters of Central America*[1] *in 1963*

Species	Life stage		Total captured	Range of standard length	Season	
	Adult	Juvenile			Spring	Fall
			Number	*Mm.*		
Lobotidae (tripletails)						
Lobotes pacificus Gilbert	–	x	3	72–246	–	x
Carangidae (jacks and scads)						
Caranx caballus Günther	x[2]	x	6,215	9–212	x	x
Caranx hippos (Linnaeus)	–	x	105	16–85	x	x
Caranx marginatus (Gill)	–	x	44	17–101	x	x
Decapterus sp.[3]	–	x	298	17–100	x	x
Elagatis bipinnulatus (Quoy and Gaimard)	–	x	218	11–263	x	x
Naucrates ductor (Linnaeus)	–	x	43	29–143	x	x
Selar crumenophthalmus (Bloch)	x[2]	x	1,348	15–108	x	x
Seriola colburni (Evermann and Clark)	–	x	5	103–154	x	–
Seriola sp.[3]	–	x	315	10–163	x	x
Coryphaenidae (dolphins)						
Coryphaena equiselis Linnaeus	–	x	5	35–68	x	–
Coryphaena hippurus Linnaeus	x[2]	x	2	34–42	x	x
Mullidae (goatfishes)						
Pseudupeneus grandisquamis (Gill)	–	x	339	26–54	x	x
Kyphosidae (sea chubs)						
Kyphosus analogus (Gill)	–	x	3	63–137	x	x
Kyphosus elegans (Peters)	–	x	22	32–103	x	x
Kyphosus sp.[3]	–	x	2	18–59	x	x
Sectator ocyurus (Jordan and Gilbert)	x[4]	x	248	17–253	x	x
Pomacentridae (damselfishes)						
Abudefduf saxatilis (Linnaeus)	–	x	437	8–46	x	x
Chromis atrilobata Gill	–	x	1,449	21–32	x	x
Scombridae (mackerels and tunas)						
Auxis thazard (Lacépède)	–	x	1	48	x	–
Euthynnus lineatus Kishinouye	x[4]	x	7	37–477[5]	x	x
Katsuwonus pelamis (Linnaeus)	x[4]	–	435	230–597[5]	–	x
Thunnus albacares (Bonnaterre)	x[4]	–	149	500–750[5]	x	–
Blenniidae (combtooth blennies)						
Blenniolus brevipinnis (Günther)	x	x	39	13–31	x	x
Stromateidae (butterfishes)						
Psenes pacificus Meek and Hildebrand	–	x	822	10–133	x	x
Mugilidae (mullets)						
Agonostomus monticola (Bancroft)	–	x	38	11–30	–	x
Mugil curema Valenciennes	–	x	6	18–47	x	x
Polynemidae (threadfins)						
Polydactylus approximans (Lay and Bennett)	–	x	30	23–47	x	x
Polydactylus opercularis (Gill)	–	x	1	40	–	x
Monacanthidae (filefishes)						
Alutera monoceros (Linnaeus)	x[2]	x	1	107	–	x
Alutera scripta (Osbeck)	x[2]	x	1	72	–	x
Balistidae (triggerfishes)						
Balistes polylepis Steindachner	–	x	9	28–184	x	x
Canthidermis maculatus (Bloch)	x	x	178	30–236	x	x

[1] Specimens cataloged in Marine Vertebrates collection, Scripps Institution of Oceanography.

[2] Adults observed but not captured.

[3] Specific name unknown.

[4] Adults collected by method other than small purse seine.

[5] Fork length.

scombrids can be ascribed to variation in collection methods rather than to seasonal differences. Adult frigate mackerel, *Auxis thazard*, black skipjack, *Euthynnus lineatus*, oceanic skipjack, and yellowfin tuna were present during both seasons, and all are known to associate with flotsam.

The mountain mullet, *Agonostomus monticola*, was not in the spring collections but occurred in 10 of the 47 fall collections. This species inhabits marine waters only as a prejuvenile (Ebeling, 1961). Thus its occurrence in only the fall collections could be due to a seasonal difference in reproductive activities.

The remainder of the species that were taken during only 1 season were relatively uncommon in the collections. Their absence during 1 season could be due to chance alone.

LIFE STAGE OF FISHES ASSOCIATED WITH FLOTSAM

Nearly all of the fishes observed and captured beneath drifting objects were juveniles; however, adult sharks, *Carcharhinus limbatus* (Müller and Henle) and *Carcharhinus azureus* (Gilbert and Starks), and schools of adult *Caranx caballus*, *Selar crumenophthalmus*, *Coryphaena hippurus*, *Sectator ocyurus*, and *Euthynnus lineatus* were observed. With the exception of *S. ocyurus*, these adults did not swim as close to the object as did the smaller fishes, and they remained near it only for short periods. None of these adults were captured by the small purse seine. Some were captured, however, by other methods. Owing to the infrequent capture of these adults and to the difficulty of ascertaining whether or not they were in fact associated with a particular object, our presentation is limited to the fishes captured by the small seine. *Canthidermis maculatus* was the only species that frequently occurred both as adult and juvenile; both stages were captured in the seine.

To determine if the size of the fishes was related to the distance of an object from shore, the shortest distance to the shore from the location of each collection was measured to the nearest nautical mile. The length measurements of species from different collections captured at the same distance from shore were combined, and a mean and range were established (figs. 2, 3, and 4).

The mean and minimum length of *Abudefduf saxatilis* and *Seriola* sp. increased with the distance of an object from shore (chi-square test for two independent samples, $p<.01$)—figs. 2 and 3. The

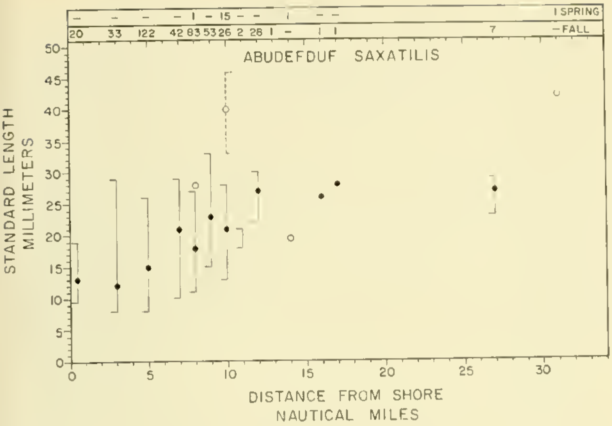

FIGURE 2.—Range and mean standard length of *Abudefduf saxatilis* collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collection, solid lines, range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall; circles without bars indicate single fish. Upper numerals are total number of *Abudefduf* captured in spring of 1963, lower numerals, fall 1963.

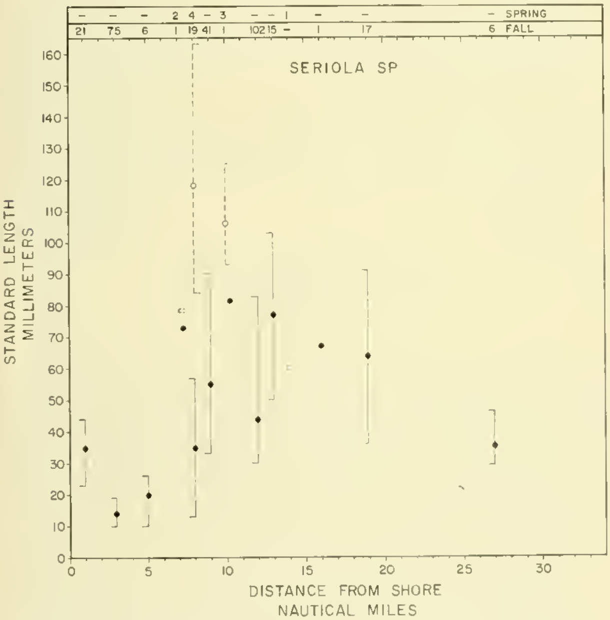

FIGURE 3.—Range and mean standard length of *Seriola* sp. collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collections, solid lines range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall; circles without bars indicate single fish. Upper numerals are total number of *Seriola* sp. captured in spring of 1963, lower numerals, fall of 1963.

maximum size of these two species did not show this change. The mean length of *Sclar crumenophthalmus* also increased with distance, but this change was not as marked as in the other two species (fig. 4).

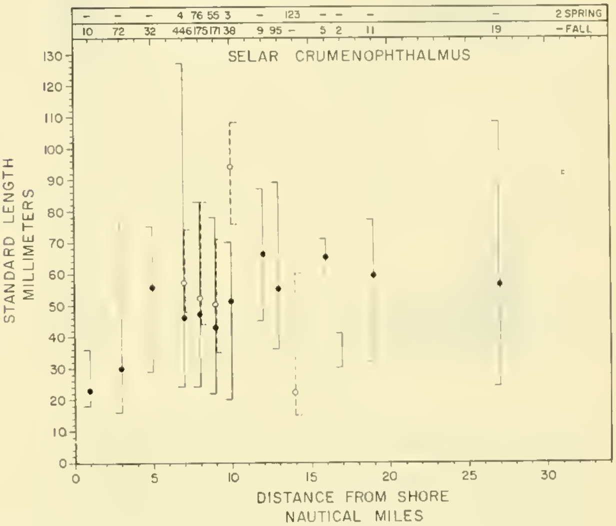

FIGURE 4.—Range and mean standard length of *Selar crumenophthalmus* collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collections, solid lines, range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall. Upper numerals are total number of *Selar* captured in spring of 1963, lower numerals, fall of 1963.

Abudefduf saxatilis spawns inshore on rocks or reefs, and the males defend the clutch of eggs (R. Rosenblatt, personal communication); thus, larvae and juveniles of this species may be more abundant inshore. It seems possible that individuals captured offshore were originally recruited to the object inshore and accompanied it as it drifted away from land. The larger size of the offshore specimens could be attributed to growth while the fish were associated with the object.

In the remainder of the fishes no obvious relation was evident between the distance from shore and the minimum or mean length; however, the ranges of sizes at which these fishes were associated with flotsam differed widely. Some species were represented by almost a complete series of juvenile stages. *Caranx caballus* and *Psenes pacificus* are good examples of this group (fig. 5). Less abundant species in this group were *Elagatis bipinnulatus*, *Kyphosus elegans*, *Sectator ocyurus*, and *Canthidermis maculatus*

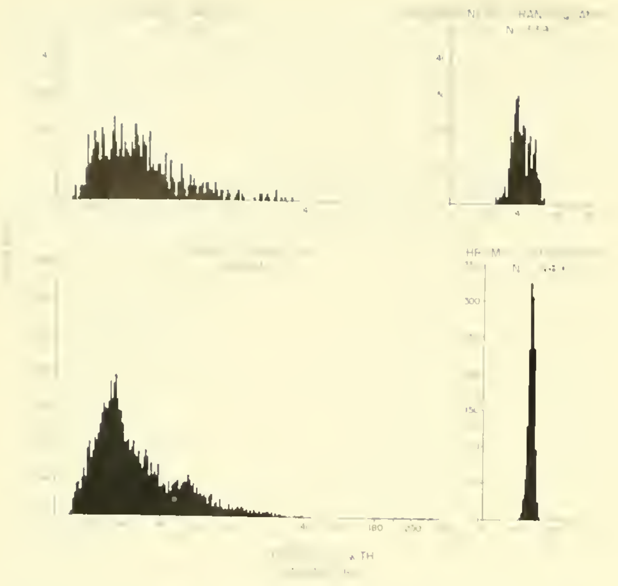

Figure 5.—Length frequency for *Psenes pacificus, Pseudupeneus grandisquamis, Caranx caballus,* and *Chromis atrilobata.* Numbers are totals for combined spring and fall collections.

(table 1). The size range of juveniles of other species was extremely restricted. *Chromis atrilobata* and *Pseudupeneus grandisquamis* had this compact type of size distribution (fig. 5). Other species, not figured, which also had a limited size range included *Agonostomus monticola, Polydactylus approximans,* and *Blenniolus brevipinnis. Pseudupeneus, Chromis, Agonostomus,* and *Polydactylus* have pelagic juvenile stages but as adults inhabit other areas. The upper size limit of these species in our collections probably was determined by the size at which they end the pelagic phase of their lives.

Blenniolus brevipinnis is a small species; females 19.5 mm. long can be sexually mature (Krejsa, 1960). Adults and juveniles have been found near drifting logs as well as among rocks and coral heads in inshore areas (Krejsa, 1960). Apparently for both adults and juveniles of this species, drifting objects are a suitable pelagic substitute for inshore habitats.

FREQUENCY, ABUNDANCE, AND DOMINANCE OF FISHES COLLECTED BENEATH FLOTSAM

The characters used by Fager and McGowan (1963) for the analysis of zooplankton populations were used to describe the structure of the flotsam-associated aggregations of fish: (1) frequency—the total number of collections in which a species occurred; (2) abundance—the range and median of the numbers of individuals per collection in which the species was found; and (3) dominance—the number of samples in which a particular species or a group including this species comprised 50 percent or more of the total number of individuals in a given collection. As the structure of the populations in the spring was similar to that in the fall, the two series of collections were combined to calculate these statistics.

Fifteen of the 32 species had frequencies greater than 10. These were ranked from 1 to 15 on the basis of their frequency, median abundance, and dominance. Tied values were given the average of the ranks (table 2 and fig. 6). The remainder of the species was ranked only by frequency (table 3).

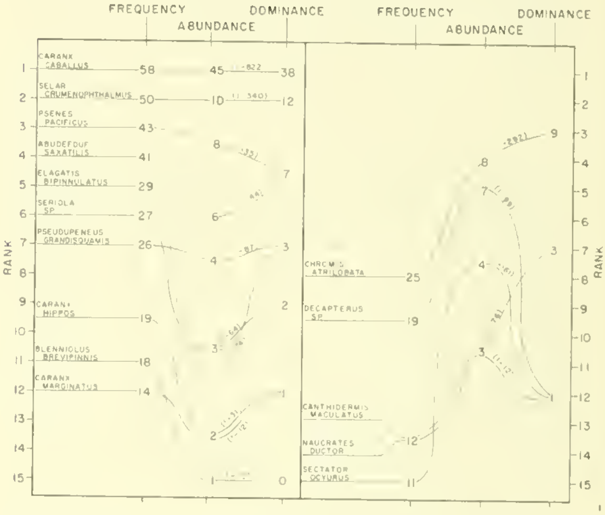

Figure 6.—Ecological characters of the 15 species most frequently captured beneath flotsam in the offshore waters of Central America in 1963. Each species was ranked separately by: *frequency,* the total number of collections in which the species occurred; *abundance,* median of the numbers of individuals per collection in which the species was found; and *dominance,* the number of collections in which a species was among those making up 50 percent of the individuals. Lines indicate the rank held by each species in the three rankings. Values upon which ranks were based are shown in each column. In the second column, parentheses enclose the range of the number of individuals per collection of occurrence. For clarity, we separated the 15 species into 2 groups: left half of figure, species whose ranked abundance was the same as or lower than the ranked frequency; and right half, species whose ranked abundance was higher than the ranked frequency. The total number of collections was 70.

TABLE 2.—*Ecological characters of the 15 most frequently captured species collected beneath flotsam in the offshore waters of Central America in 1963*[1]

Species	Frequency[2]	Rank[3]	Abundance		Rank[3]	Dominance[4]	Rank[3]
			Range[5]	Median[6]			
Caranx caballus	58	1	(1–822)	45	1	38	1
Caranx hippos	19	9.5	(1–31)	2	13.5	1	12
Caranx marginatus	14	12	(1–12)	2	13.5	1	12
Decapterus sp.	19	9.5	(1–99)	7	5	1	12
Elagatis bipinnulatis	29	5	(1–64)	3	10.5	2	9
Naucrates ductor	12	13.5	(1–12)	3	10.5	1	12
Selar crumenophthalmus	50	2	(1–340)	10	2	12	2
Seriola sp.	27	6	(1–74)	3	10.5	3	7
Pseudupeneus grandisquamis	26	7	(1–87)	4	7.5	3	7
Sectator ocyurus	11	15	(1–161)	4	7.5	1	12
Abudefduf saxatilis	41	4	(1–44)	6	6	7	4.5
Chromis atrilobata	25	8	(1–292)	8	4	9	3
Blenniolus brevipinnis	18	11	(1–10)	1	15	0	15
Psenes pacificus	43	3	(1–135)	8	3.5	7	4.5
Canthidermis maculatus	12	13.5	(1–176)	3	10.5	3	7

[1] The total number of collections was 70.
[2] The total number of collections in which the species occurred.
[3] Rank based on figures in adjacent columns.
[4] The number of samples in which a particular species or a group including this species comprised 50 percent or more of the total number of individuals in a given collection.
[5] Range of the numbers of individuals per collection in which species was found.
[6] Median of the numbers of individuals per collection in which species was found.

TABLE 3.—*Frequency, abundance, and dominance of species occurring in 10 or fewer collections made in the offshore waters of Central America in 1963. Listed in order of frequency*

Species	Frequency	Abundance[1]	Dominance
Agonostomus monticola	10	1 (1–11)	0
Polydactylus approximans	9	1 (1–12)	0
Kyphosus elegans	8	1 (1–12)	0
Mugil curema	5	1 (1–2)	0
Balistes polylepis	5	1 (1–4)	0
Kyphosus analogus	3	1 (1)	0
Lobotes pacificus	3	1 (1)	0
Seriola colburni	2	– (2–3)	0
Coryphaena hippurus	2	– (1)	0
Coryphaena equiselis	2	– (2–3)	2
Kyphosus sp.	2	– (1)	0
Polydactylus opercularis	1	– (1)	0
Auxis thazard	1	– (1)	0
Euthynnus lineatus	1	– (1)	0
Alutera manoceros	1	– (1)	0
Alutera scripta	1	– (1)	0

[1] Figures in parentheses show range in number of individuals per collection of occurrence.

Nine of the 32 species were carangids, and all but 1 of these, *Seriola colburni*, were among the 15 most frequent species. The carangid, *C. caballus* was by far the most frequent, abundant, and dominant species collected. This fish contributed 50 percent or more of the individuals in more than half of the collections. *Selar crumenophthalmus*, also a carangid, ranked second in frequency, abundance, and dominance. No other family was represented as frequently in the collections. The family Kyphosidae was represented by four species but only one, *Sectator ocyurus*, occurred in more than 10 collections.

On the basis of their rank by frequency, abundance, and dominance, the 15 most frequent species can be divided into three groups: (1) species that occupied about the same rank in all three categories; (2) species that were captured frequently but were not abundant in the collections in which they occurred; and (3) species captured less frequently that were abundant in the collections in which they occurred. The three highest ranking species, *C. caballus*, *Selar crumenophthalmus*, and *Psenes pacificus* were in the first group. *Abudefduf saxatilis* and *Blenniolus brevipinnis* exemplify the second group, and *Chromis atrilobata* and *Canthidermis maculatus* the third.

The factors responsible for the differences in frequency and abundance of species are unknown. For some species, evidence suggested that schooling was a significant factor. All of the 15 most frequently captured species, except *Abudefduf* and *Blenniolus*, schooled either with their own or other species beneath flotsam. *Abudefduf* remained near the object and appeared to defend small territories; *Blenniolus* maintained contact with the surface of the object and were not aggregated. Possibly the solitary or individual habits of these species were responsible for their lower abundance. Juvenile *Chromis* school at the stage at which they associate with flotsam. This species was dominant in seven of eight collections made in the same area on the same day. The median number of individuals in these seven collections was 199. *Chromis* was dominant only once in the remainder of the collections, and the median number of fish per collection was two. The irregular abundance of *Chromis* could be ascribed to a tendency toward the recruitment of an entire school.

Canthidermis maculatus also was a schooling species and tended to be abundant in the collections in which it occurred. This species did not show the limited temporal and regional abundance described for juvenile *Chromis*, but the distribution of *Canthidermis* appeared to extend farther to sea than other species. The collection farthest from shore (200 nautical miles) contained 87 *Canthidermis* and 4 *Balistes polylepis*. Only *Canthidermis* was observed beneath other drifting material in the same area. The four *B. polylepis* were located inside the cavity of a large bamboo stem and probably did not represent a usual component of high-seas aggregations. Had we taken more collections from flotsam drifting 100 or more nautical miles from shore we feel the frequencies for *Canthidermis* would have increased proportionately.

Decapterus sp. ranked fifth in abundance but only once dominated a collection. This species nearly always schooled with *Selar crumenophthalmus* but was less abundant in the mixed schools. *Decapterus* was captured without *Selar* in only 7 of 19 collections. Thus whenever a large number of *Decapterus* was taken, the number of *Selar* was usually larger. Hence, *Decapterus* rarely dominated a collection.

The use of only the numbers of individuals for the determination of dominance instead of numbers and weights obscured some of the relations among species. Had weights as well as numbers been used, *Canthidermis* and *Psenes* probably would have dominated more collections and *Chromis*, *Pseudupeneus*, and *Abudefduf* fewer. Owing to their large size range and abundance, little difference would be expected in the values for *C. caballus* and *Selar*.

OBJECT SIZE

To determine if the length or the number of fishes was related to the size of the object, we recorded for each collection the volume of the object in cubic centimeters, the total number of fishes captured, and the mean length of all fishes in the collection. Of the two variables only the number of individuals in the collection was obviously related to the volume of the object. Collections made beneath large objects tended to be larger than those taken beneath smaller objects (table 4).

Field observations indicated that the frequency of occurrence of larger fishes may be related to the size of the object. The largest object studied, an entire tree, was too large to be encompassed by the purse seine. The tree was 1 m. in diameter at the root section, had a trunk diameter of 0.3 m. and was over 10 m. long. Associated with the tree was the largest aggregation of adult fishes seen during the study. There were large schools of adult *Sectator ocyurus*, *Canthidermis maculatus*, *Coryphaena hippurus*, and *Euthynnus lineatus* in addition to numerous juvenile fishes. A portion of the school of adult *Sectator* is shown in figure 7A, and in 7B some of the adult *Canthidermis* are shown among the branches of the tree. For comparison, two groups of juvenile fishes that were associated with two smaller objects are pictured in 7C and 7D. Yabe and Mori (1950) captured, by hook and line, fishes associated with a tree of similar dimensions (1 m. in diameter at the butt and 15 m. long). The lengths of the fish of the species they captured exceeded the lengths of the fish in our purse seine collections by about a factor of 10. In our study, the juvenile fishes that were associated with the tree were of the same species and about the same size as those collected beneath smaller objects. Thus the size of the object appeared to be related to the presence or absence of large or adult fishes rather than differences among juveniles.

TABLE 4.—*Number of collections made of fishes associated with objects of three size classes and the number of fishes these collections contained*

[Collections were made in the offshore waters of Central America in 1963]

Fish in collection	Collections from objects of different volume (cubic centimeters)			Total
	101-5,000	5,001-100,000	100,001-5,000,000	
Number	Number	Number	Number	Number
1-10	5	3	0	8
11-100	2	14	6	22
101-1000	0	19	19	38
Total	7	36	25	68[1]

[1] Two collections omitted owing to lack of volume measurements.

ARTIFICIAL MOORED OBJECTS

To study the rate of recruitment of fishes to floating materials, eight objects of various types were moored near the Costa Rican coast for periods of 15 hours to 46 days. Six objects were not visited from the time they were moored until the day the collection was made. Two balsa logs were moored in the same locality at the same time and were observed daily until collections were made on the fifth day.

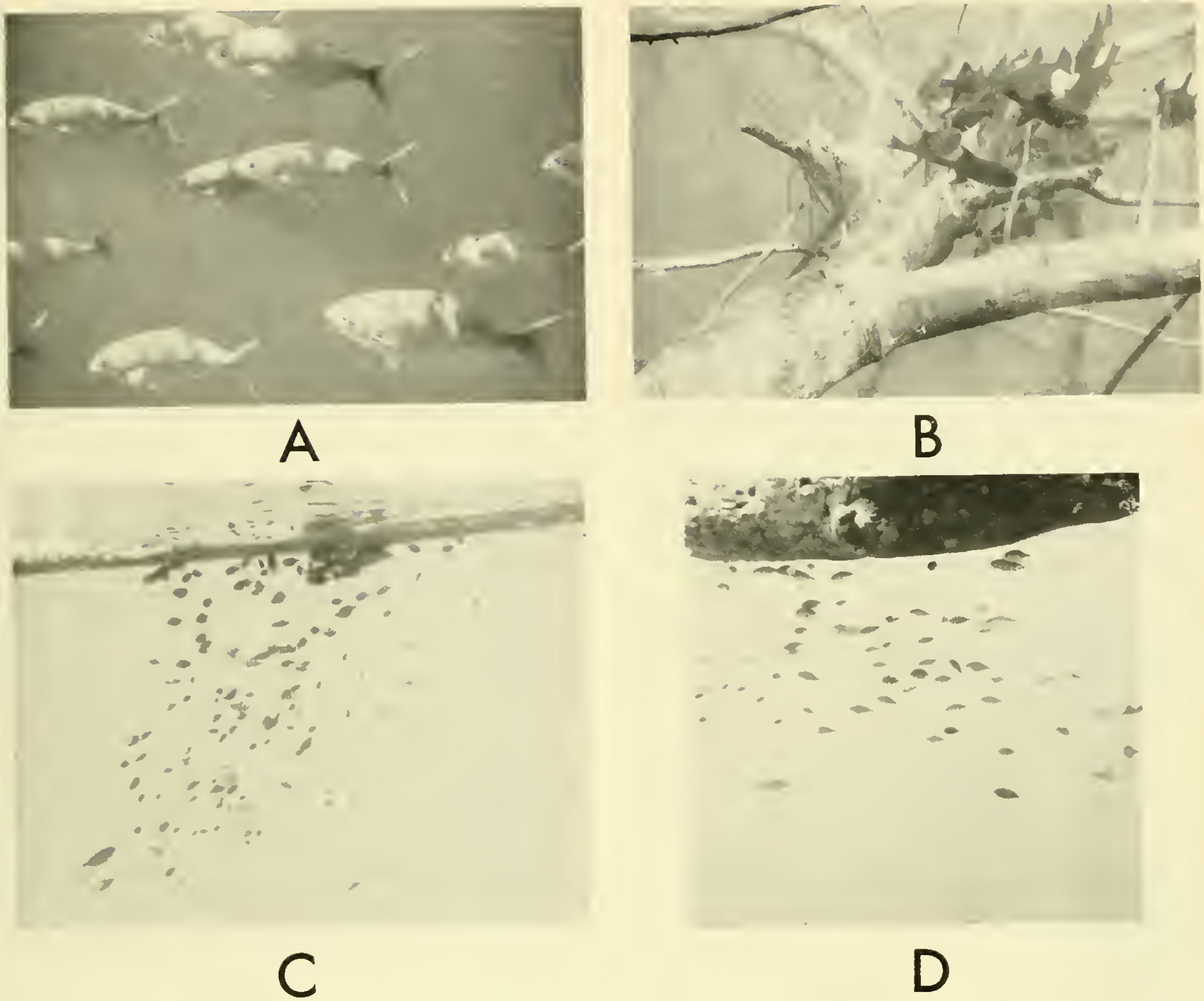

FIGURE 7.—Fishes associated with drifting objects in the offshore waters of Central America in 1963. A, a school of adult *Sectator ocyurus* associated with an entire tree; the small fish in background were juvenile *Selar crumenophthalmus*. B, an aggregation of adult *Canthidermis maculatus* in the branches of the same tree; all but three had a dark coloration. C, a group of juvenile *Psenes pacificus*, *Naucrates ductor*, and other carangids beneath a drifting plank; *Psenes* are in a dense clump directly below the plank, *Naucrates* can be recognized by the presence of dark vertical bars. D, juvenile *Canthidermis maculatus*, *Naucrates ductor*, and various juvenile carangids beneath a drifting log.

Divers made daily counts of the number of individuals of each species beneath each of the two logs. The volumes of the two balsa logs calculated from their measurements were 0.021 m.^{3} (log A) and 0.065 m.^{3} (log B).

Counts of the number of individuals beneath logs A and B were 20 and 96 for the second day and 121 and 80 for the third day. By the fourth day it was not possible to make an accurate tabulation because the number of fish under each log was well over 100. On the fifth day 198 individuals were captured under log A and 349 under log B. Prior to being moored log B was encountered 27 miles from shore and 236 fish representing 8 species were captured at that time. Thus more fish were captured after the log was moored 5 days than were collected when the log was drifting 27 miles from shore. Fewer species were represented, however. The larger number of individuals captured beneath log B may reflect the difference in volume of the logs.

Although logs A and B were moored only 100 m. apart, their associated fish populations differed in species composition, dominant species, and the time at which each species was first observed. No ordered recruitment of species was evident (table 5).

The number of fish collected beneath inflated truck inner tubes varied greatly (table 6). All the tubes were identical in size and shape with the exception of the tube that had 10 manila lines attached. After periods longer than 5 days the number of fish collected beneath the tubes did not increase substantially with time through 20 or more days. The number of fish appears to increase rapidly during the first few days and thereafter to remain at about the same level.

Because a drifting object passes through inshore spawning areas, juveniles of species that spawn inshore would be expected to be more abundant beneath a drifting object than beneath an object moored offshore. *Abudefduf saxatilis* and perhaps *Seriola* sp. spawned inshore. Both species showed a high frequency in the fall collections, but neither was found under the two balsa logs moored in the fall. With these two exceptions, no difference existed in the species composition or in the size of the individuals between populations of fishes associated with moored objects and those associated with drifting objects.

TABLE 5.—*Species recruited to two balsa logs, A (volume, 0.021 $m.^3$ and B (volume, 0.065 $m.^3$) moored 100 m. apart 7 nautical miles from the Costa Rican coast in 1963*

Species	Log A		Log B	
	Day species first observed[1]	Fish captured on fifth day	Day species first observed[1]	Fish captured on fifth day
		Number		*Number*
Pseudupeneus grandisquamis	3	87	2	31
Selar crumenophthalmus	3	79	3	304
Caranx caballus	2	17	2	129
Chramis atrilobata	3	8	3	0
Elagatis bipinnulatus	5	6	4	6
Psenes pacificus	–	–	5	2
Blenniolus brevipinnis	5	1	–	–
Caranx marginatus	2	0	4	2
Polydactylus approximans	3	0	3	0
Alutera	–	–	4	0
Total		198		474

[1] No underwater observations were made on the day the log was moored (Day 1).

TABLE 6.—*Number of fish and species recruited to various objects moored near the Costa Rican coast in 1963*

Object	Time elapsed after establishment	Fish	Species	Distance from shore	Season
		Number	*Number*	*Nautical miles*	
Truck inner tube[1]	15 hours	203	6	31	Spring
Balsa log (A)	5 days[2]	198	7	7	Fall
Balsa log (B)	5 days[2]	474	6	7	Do.
Truck inner tube	6 days	263	8	8	Spring
3 feet by 3 feet by ¼ inch plywood	20 days	2	1	2	Fall
Truck inner tube	20 days	13	4	7	Spring
Truck inner tube	28 days	492	7	8	Do.
Truck inner tube	46 days	118	5	9	Do.

[1] Attached to this inner tube were ten ¾-inch (19 mm.) manila lines 10 m. long. All tubes had a volume of 0.286 $m.^3$

[2] Established at same time at same locality.

BEHAVIOR

DISTRIBUTION AND FRIGHT BEHAVIOR

When disturbed, nearly all species swam toward the drifting object and maintained a position much closer to it than when undisturbed. The fishes showed this behavior when a school of porpoise, *Stenella grafmani*, passed a log, when four porpoise, *Tursiops* sp., passed nearby, when a school of black skipjack approached a log, and when a shark, *Carcharhinus azureus*, swam beneath a log. The movements of a diver, skiff, and the research vessel also induced this response. The fishes rapidly habituated to the movement of the outboard skiff; after several passes of the skiff near the same log the fear reaction no longer could be evoked.

Most species showed a marked change in behavior when disturbed. *Abudefduf saxatilis* frequently entered holes or crevasses on the surface of the log. The kyphosids moved in and out of holes and swam back and forth rapidly over the log so close to it that their fins almost touched it. Schools of all species became more compact; sometimes individuals that were a part of a diffuse aggregation of several species separated into monotypic schools. For example, when only a few *Chromis atrilobata* were present under undisturbed conditions they remained with the carangids in a loose aggregation, but when frightened they formed a compact monotypic school.

The fear response produced a marked vertical stratification of species beneath the object. Species distributed at various distances from the log, or members of a common loose aggregation, separated into discrete compact groups. If large numbers of fishes were grouped in this manner the distribution usually resembled a cone, the apex of which was at the underside of the object. The base was usually formed by a large group of juvenile *Selar crumenophthalmus* and *Decapterus* sp. The fish were always in this position when the object was approached by the research vessel or the skiff. It was only after the skiff had been near the log for a half hour or longer that the fish lost these more rigid groupings and strayed from their position directly beneath the log.

When the fish were undisturbed, the conical distribution beneath the log was not apparent, owing to movements in the horizontal plane and the breaking up of groups. The mixed school of *C. caballus*, *C. hippos*, *C. marginatus*, *Elagatis bipinnulatus*, and *Psenes pacificus* broke up into smaller units, and these at times moved at least 15 m. away from the object. Juvenile kyphosids swam 1.5 to 3 m. away from the object but did not range as far as the juvenile carangids. Adult *Canthidermis maculatus* frequently swam beyond the limit of visibility—15 m.—and returned to the object. *Abudefduf saxatilis* and *Blenniolus brevipinnis*, on the other hand, always remained near the object.

The relative vertical position of species usually was maintained under both disturbed and undisturbed conditions. Those species that increased their horizontal range when undisturbed also increased, to a lesser extent, their vertical range of movements. The juvenile kyphosids swam as deep as 1.5 m. below the object; *Pseudupeneus*, *Decapterus*, and *Selar* were observed at a depth of 12 m. (limit of visibility from the surface). Adult *Canthidermis* was the only species whose relative vertical position changed markedly. Under disturbed conditions this species was often among those occupying a position close to the object, but after the disturbance had ceased they ranged from the surface to depths over 12 m. Juvenile *Canthidermis*, on the other hand, occupied the same relative vertical position under disturbed and undisturbed conditions.

Commonly the responses of juvenile fish to a drifting object differed from those of the adult. Adults swam deeper, ranged farther, and appeared beneath the object less frequently than did juveniles. With the exception of adult *Sectator* and *Canthidermis*, they did not always respond to movements of the skiff by moving toward the object as did all the juvenile fishes. It was not possible, therefore, to be certain that adult *Euthynnus lineatus*, *Coryphaena hippurus*, *Caranx caballus*, or *Selar crumenophthalmus* were truly associated with a particular object.

POSITION RELATIVE TO OBJECT AND LATERAL BODY COLORATION

The lateral coloration of the fishes and their position relative to the object were correlated. The species that remained closest to the log were darker than were those that maintained greater distances from the object or associated with the object only intermittently (table 7). For example, *Abudefduf saxatilis*, *Psenes pacificus*, all species of *Caranx*, the kyphosids, *Blenniolus brevipinnis*, and *Lobotes pacificus*, were yellow, brown, or black and remained near the log. On the other hand, *Chromis atrilobata*, brownish above, silvery below, occupied a deeper position, and *Selar crumenophthalmus* and *Decapterus* sp., which were silvery, regularly occupied the

Table 7.—*Lateral coloration (live), estimated vertical distribution and aggregation type of certain species associated with flotsam in the offshore waters of Central America in 1963*

Fishes[1]	Lateral coloration (live)	Estimated vertical distance from object[2]	Grouping
Juvenile:			
Blenniolus brevipinnis	Dark brown with black bars	0	Individual
Abudefduf saxatilis	Yellow with dusky bands	0–3	
Canthidermis maculatus	Blue with white spots to black	3	
Polydactylus approximans[3]	Silvery below, blue above	3	Pure school
Kyphosus analogus	Black with pale purple stripes and spots	0–15	Individual
Kyphosus elegans	Black with pale purple stripes and spots		
Sectator ocyurus	Yellow with brown stripes below, dark olive green above	15–150	Mixed school
Caranx caballus	Yellow below, olive above		
Caranx hippos	Yellow with dark dusky bands		
Caranx marginatus	Yellow with dark dusky bands		
Elagatis bipinnulatus	Yellow with two blue stripes below, dark bluegreen above		
Seriola sp.	Yellow with black bands below, dark olive above		
Psenes pacificus	Yellow with brown stripes below, olive above		
Chromis atrilobata	Silvery below, pale brown above	150–200	Pure school
Decapterus sp.	Silvery below, blue above	150–600	Mixed school
Selar crumenophthalmus	Silvery below, blue above		
Pseudupeneus grandisquamis	Silvery below, blue above		
Adult:			
Canthidermis maculatus	Blue with white spots to black	0–300	Pure school
Caranx caballus	Silvery below, blue above	600–1300	

[1] Only those species are included for which we have sufficient notes on vertical distribution.
[2] Estimate made under disturbed conditions.
[3] Did not school beneath log but to one side near the surface.

deepest position of all the permanently associated fishes. This relationship suggests a protective advantage afforded by the log other than the physical obstruction of predators. The dark brown, yellow, and black of the closely associated species was well adapted to the colors of the most commonly occurring flotsam. Thus, when associated with flotsam, the more darkly colored species were probably less conspicious to predators than when isolated. From examination of fishes associated with flotsam in the Atlantic, Murray and Hjort (1912) made similar speculations. They also suggested that *Naucrates ductor*, blue with darker transverse bars, might occupy an intermediate position between the organisms strongly associated with flotsam and those which merely live near drifting objects.

Although both *Canthidermis maculatus* and *Polydactylus approximans* had a pelagic coloration, they were frequently near the object when frightened. The fright reaction of *Polydactylus* differed from that of other species. These fish formed a compact rapidly moving school a few centimeters below the water surface. The school moved about near the object but never below it. Adult *Canthidermis* when undisturbed swam deeper and ranged farther from the object than all the yellow, brown, and black species. When frightened they moved to 0 to 3 m. below the object. Thus, this species occupied a position in keeping with its pelagic coloration only under undisturbed conditions. *Canthidermis* has the ability to turn from the normal pelagic coloration, blue with white spots, to black. Juveniles and adults had intermediate color phases as well as pelagic and dark phases.

Within the same species, coloration appeared to reflect differences in the behavior of association. The silvery adult *C. caballus* did not maintain close contact with an object and appeared beneath it only intermittently. The yellowish juvenile *C. caballus*, on the other hand, maintained close contact with the object. Gooding and Magnuson (see footnote 1) reported that when *Psenes pacificus* was associated with their raft it was yellow, but unassociated individuals were silvery.

FEEDING BEHAVIOR

Adult *Canthidermis*, *Alutera*, and juvenile *Elagatis* frequently were seen feeding on colonial salps. Once we saw three *Canthidermis* nipping the base of the neck and legs of a green turtle. On no other occasion did we see this species engaged in activities that could be interpreted as parasite cleaning. Occasionally juvenile kyphosids were observed snapping at the surface of a log or branch. Juvenile *Abudefduf* showed this behavior more frequently.

Adult *Coryphaena hippurus* frequently pursued smaller fishes located beneath flotsam. We did not see them capture fish, but the stomach of an adult *Coryphaena* taken by hook and line contained a *Caranx caballus*. Frequently fishes with lateral lesions were seen beneath logs. These included *Caranx caballus*, *Canthidermis maculatus*, and *Elagatis bipinnulatus*.

Two schools of skipjack, and one of yellowfin tuna were associated with logs in the study area and were seined by American tuna fishermen. When the boats reached port, stomach contents of fish from each school were examined and the lengths of the fish determined. Euphausiids and myctophids were the dominant food organisms in the stomachs of skipjack, and the portunid crab, *Portunus affinis*, in the stomachs of yellowfin tuna. Only seven stomachs contained fishes—carangids and scombrids—that may have been associated with flotsam (table 8). Stomachs from each of the three schools contained debris of the kind usually found near drifting logs (pieces of wood, thorns, and bird feathers).

TABLE 8.—*Occurrence of flotsam-associated fishes in the stomachs of two schools of oceanic skipjack, and one school of yellowfin tuna associated with flotsam in offshore waters of Central America in 1963*

Stomach contents	*Skipjack* seined October 3, 1963 (222-48)[1]		*Skipjack* seined October 6, 1963 (213-61)[1]		*Yellowfin tuna* seined June 18-22, 1965 (149-107)[1]	
	Number	*Volume Ml.*	*Number*	*Volume Ml.*	*Number*	*Volume Ml.*
Fish						
Flotsam-associated species	0	0	1	77.0	6	575.0
Unassociated species	10	281.1	34	1448.5	7	206.0
Unidentified remains	3	0.3	0	0	44	790.0
Invertebrates	33	212.8	26	25.0	73	1579.0
Bird feathers and plant debris	5	—	2	—	3	—

[1] At left, number examined; at right, number with food.

COURTSHIP BEHAVIOR

No eggs of any kind were found attached to the flotsam. Some species observed near drifting objects were, however, in reproductive condition. Three ripe male black skipjack were captured from a school near a large drifting tree. Underwater observations of these fish revealed a high frequency of wobbling and chasing. This behavior was similar to that described by Magnuson and Prescott[3] for the reproductive behavior of Pacific bonito, *Sarda chiliensis* (Cuvier).

Nearly all the adult male and female *Canthidermis maculatus* captured in the fall were ripe. On one occasion these fish showed what may have been courtship behavior, but no spawning was observed.

TRANSFER OF FISHES TO OTHER OBJECTS AND HOMING

Some species were attracted to the skiff when it drifted alongside a floating object. Only the fishes that occupied upper positions in the aggregation, such as juvenile *Caranx caballus*, *Psenes pacificus*, *Elagatis bipinnulatus*, *Kyphosus elegans*, and *Sectator ocyurus*, showed this behavior. The more deeply positioned species, *Selar crumenophthalmus*, *Decapterus* sp., *Pseudupeneus grandisquamis*, and *Chromis atrilobata* did not transfer to the skiff. Those species most closely associated with the surface of the object, *Abudefduf saxatilis* and *Blenniolus brevipinnis*, did not transfer unless the original object was removed from the water. Transfers to the skiff were only temporary. The fishes swam beneath the skiff, remained there a few minutes, and then returned to the original object. Movements back and forth from the object to the skiff lasted no longer than 30 minutes; thereafter, the fish remained beneath the original object.

Two attempts were made to transfer the fish population of a log to a 4- by 8-foot (122 cm. by 243 cm.), 1/4-inch (6 mm.) thick plywood sheet. A log with a fish population was attached to the plywood sheet 24 hours; then the two objects were separated. During daylight, underwater observations were made while the two objects were attached and after they were parted. At no time did the fishes congregate beneath the plywood sheet. They remained beneath the original object during the 24 hours the objects were attached and after they were separated. The experiment was repeated; this time, 60-cm. sections of unraveled 1/2-inch (13 mm.) manila line were attached at 10-cm. intervals in three rows to the underside of the plywood. The rope produced a dense mass of filaments. After 2 1/2 hours none of the fishes had transferred from the original log to the plywood, but 1 hour after the plywood was freed from the original object, over 100 *C. caballus* had been recruited to the plywood.

The failure of fishes to form a permanent association with new objects, a skiff or plywood sheet, when already associated with another object suggests that a more familiar object may have a higher valence.

Ten adult *Canthidermis maculatus* were captured, tagged, and released separately; four were released 7.5 m. from their original log, four at 15 m. and two at 30.5 m. One hour and 30 minutes later, three of those released at 7.5 m. and three released at 15 m. had returned. Neither of the fish released at 30.5 m. returned. Conceivably the fish planted at the greatest distance could not see the log. The recapture of fish planted at lesser distances suggested that they may return to their log when it is within visual range.

RUBBING BEHAVIOR

Adults of *Coryphaena hippurus*, *Canthidermis maculatus*, and *Sectator ocyurus* frequently rubbed their dorsal surface or sides against the logs and the skiff. An entire school of adult *Sectator* showed this behavior.

SEA SNAKES

We frequently observed the sea snake, *Pelamis platurus*, swimming near the surface. Often a small school of fish of the genus *Polydactylus* was below a snake. On three occasions the snake was feeding. It began to swim backwards; the schooled fish reversed direction and began swimming with their heads oriented toward the tail of the snake. The snake then captured fish from the school by a rapid thrust of the head and anterior portion of the body, directed either to the side and posteriorly or downward and posteriorly.

Klauber (1935) also observed *P. platurus* feed on fish schooled beneath it.

Klawe (1964) examined the stomachs of 56 *P. platurus* from the eastern tropical Pacific. In the 22 which contained food, *Polydactylus approximans* was the most abundant food, *Pseudupeneus grandisquamis* was second, and Mugilidae third. One individual each of *Selar crumenophthalmus*, *Caranx hippos*, and *Fistularia corneta* also were found. Except for *F. corneta* we captured all of these species beneath flotsam, and there was no difference in size between the fishes we collected and those in the stomachs of sea snakes. Apparently *P. platurus* takes advantage of the habit of some species to congregate beneath flotsam.

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[3] John J. Magnuson and John H. Prescott—Courtship, locomotion, feeding, and miscellaneous behavior of Pacific bonito (*Sarda chiliensis*). Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

ECOLOGICAL INTERPRETATION

Fishes were recruited rapidly to moored objects. The number beneath objects moored 5 days and the number beneath those moored 20 or more days did not differ. Goose barnacles were attached to all four objects moored 14 days or longer, but they were found on only one drifting object. Thus, all but one of the drifting objects probably had been at sea not longer than 14 days. Rapid recruitment appears to be characteristic of the formation of flotsam-associated fish aggregations. Hardenberg (1950) reported that Indonesian fishermen harvest the fishes beneath their palm frond rafts at intervals of several days. Gooding and Magnuson (see footnote 1) stated that fishes were recruited to their raft minutes after it was set adrift.

Recruitment of fishes followed no particular sequence. Small collections containing only a few fish were not necessarily all of one species. The species composition and order of recruitment of fishes to two balsa logs moored 100 m. apart were dissimilar.

The same species dominated our collections in both fall and spring. Similarities were marked between the families and genera represented in our study area and those reported from other areas (Uchida and Shojima, 1958; Besednov, 1960; Kojima, 1960a; Mansueti, 1963). Juvenile carangids were by far the most important family in terms of abundance, number of species, and dominance. They were also by far the most frequently reported flotsam associate from other areas. Other families of fishes commonly encountered in this study and frequently reported by other authors included the Scombridae, Balistidae, Kyphosidae, and Stromateidae.

The presence of attached invertebrates on floating objects appeared not to influence the occurrence of fish species. The only drifting object that had goose barnacles attached did not have a species composition different from that of objects without the barnacles. Although barnacles were present on each of four objects moored 14 or more days, the species composition of the aggregations of fish did not differ from those of objects moored much shorter periods.

Many of the flotsam-associated fishes were schooling species. We believe that the habit of schooling and of association with drifting materials may be related. Two scombrids, *Katsuwonus pelamis* and *Thunnus albacares*, not only associate with inert materials but also with large sharks and whales, and *T. albacares* is a common associate of porpoise schools (Uda and Tsukushi, 1934; and unpublished logbook records of the Inter-American Tropical Tuna Commission). The carangid, *Naucrates ductor*, known for its association with sharks (Dales, 1957), also was found beneath flotsam in this and in other studies (Murray and Hjort, 1912; Galea, 1961). Many fishes school at times with fish other than their own species. *Katsuwonus pelamis* and *Thunnus albacares* school together (Orange, Schaefer, and Larmie, 1957), and juvenile *Selar crumenophthalmus* and *Decapterus* sp. were observed schooling together in this study. *Trachurus symmetricus* (Ayres), a carangid associate of flotsam in southern California waters, schools with *Scomber japonicus* Houttuyn and *Sardinops sagax* (Jenyns)[4] and associates with jellyfish (Limbaugh, 1955). The tendencies of fishes to associate with living animals other than their own species and to associate with inert drifting materials may be related. Atz (1953) suggested, among other possibilities that an aggregating companion for a schooling fish could represent merely "a simple point of reference for optical fixation". Flotsam could function in this capacity for schooling fishes.

A schooling mechanism cannot explain the presence of all the associated species. Some fishes did not school, and for others alternative mechanisms are equally plausible. Mechanisms postulated by other authors were: attraction to food, negative phototactic response to the shadow of the object, shelter from predators, presence of spawning substrate, and parasite-cleaning symbiosis.

Owing to the infrequent occurrence of flotsam-associated fishes in the stomachs of predators the food hypothesis probably can be eliminated for predacious adults.

For juveniles and nonpiscivorous adult fishes the food hypothesis would not apply, as the drifting materials were usually devoid of attached invertebrates and algae that would provide food. That fishes were attracted because plankton was more visible in the shadow cast by the object also seems unlikely, because the fishes did not remain in the shadow. Furthermore, plywood sheets that cast large shadows were less effective in attracting fish than were objects that produced smaller shadows.

That all the juvenile fishes and adult *Canthidermis maculatus* and *Sectator ocyurus* swam toward and beneath the object when predators appeared, suggests the association has a selective advantage. This behavior was not, however, a mechanism for the association, because fishes remained near the object in the absence of predators.

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[4] Unpublished data, Bureau of Commercial Fisheries, La Jolla, California.

Use of the object as a spawning substrate would apply only to adult fishes. Adults, however, represented only a small portion of the total individuals present. Adults of two species, *Euthynnus lineatus* and *Canthidermis maculatus*, were in reproductive condition. *Euthynnus* does not have attached eggs, however (Calkins and Klawe, 1963), and no eggs were found on any of the floating materials.

The cleaning-station hypothesis suggested by Gooding and Magnuson (see footnote 1) could apply only to some of the fishes. *Canthidermis maculatus* alone showed behavior that could possibly be interpreted as cleaning. This species was taken in only 14 of the 70 collections. Except in the collection made farthest from shore, where *Canthidermis* and *Balistes polylepis* were the only species present, no differences in the species composition were evident in the collections that contained *Canthidermis*. Thus, if *Canthidermis* regularly consumes parasites of other fishes the activity does not appear to influence the presence of these fishes.

Artificial reefs established in sandy locations rapidly attract groups of fishes that would not otherwise inhabit these areas (Carlisle et al., 1964). The artificial reef provides the habitat requirements for certain fishes in an otherwise unsuitable area. Similarly, a drifting object may provide a suitable habitat for inshore fishes that have pelagic juvenile stages or that have become displaced from shore. This explanation seems to be plausible for the presence of *Abudefduf saxatilis*, *Blenniolus brevipinnis*, *Balistes polylepis*, and other species. The very restricted size range of *Chromis atrilobata* and *Pseudupeneus grandisquamis* suggests that these species are available for association during a limited period. Many of the *Pseudupeneus* were near the size at which metamorphosis takes place. Approaching metamorphosis was indicated by the slight color changes in some of the individuals and by pronounced changes in coloration after the fish were kept in a shipboard aquarium 34 hours. Possibly large premetamorphic juveniles may be attracted to objects because of changes associated with metamorphosis; for these fish the object may represent an inshore or nonpelagic habitat.

In summary, we found little evidence to support the mechanisms postulated by other authors. We have suggested two mechanisms: (1) fishes are attracted to drifting materials because the object functions as a schooling companion, and (2) for species not adapted to a pelagic life and others undergoing a change from a pelagic to other modes of existence, drifting materials may function as a substitute for a reef or other substrate. In both situations the object may have the same function, that is, provide a visual stimulus in an optical void.

The occurrence of juvenile fishes beneath flotsam was much more frequent than that of adults. That some species, as *Chromis atrilobata*, *Pseudupeneus grandisquamis*, and *Agonostomus monticola*, are pelagic only as juveniles can explain the absence of the adults. Of the species that are pelagic as juveniles and adults, the juveniles were in the vicinity of an object for longer periods and remained closer to the object than did the adults. Owing to their larger size and faster swimming speed, adults are probably less susceptible to predation. Thus, for adult fishes the selective advantage of maintaining a close association with a drifting object may be small. It is also possible that development is accompanied by an increase in the specificity of the responses of schooling fishes to other schooling companions. The valence of flotsam as a schooling object would then be lowered and intermittent association with drifting objects might be expected.

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ANALOG COMPUTER MODELS OF FISH POPULATIONS

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ABSTRACT

A modern analog computer, together with an X–Y plotter,[1] provides a means of constructing useful models of commercially exploited fish populations. The model combined conventional exponential fishing and natural mortality rates with a Gompertz curve of growth in weight. By combination of these rates and curve into a single differential equation, survival curves for successive year classes of fish were generated by the computer and plotted by the plotter. Weights for all year classes present in each season were summed graphically. Recruitment was determined from a stock-recruitment curve, set into a function generator of the computer. Yields for each season were calculated by multiplying stock weight by rate of exploitation and were compared with actual yields to test the validity of the models.

The technique was demonstrated by use of empirical and hypothetical data for the Atlantic cod (*Gadus morhua*). It is generally applicable to fisheries for which good measures of total catch, growth rate, natural and fishing mortality rates, and stock-recruitment relation are available.

It is important to use reasonable values of biological variables in constructing the models because it was not possible to demonstrate beyond doubt that the set of parameters for any given model provides a unique solution.

Compared with other techniques, the analog-graphic approach offers low cost of equipment, moderate computation speed, ready accessibility of equipment, and good visibility of results during computation. It is limited in accuracy (two or three digits) and in scaling requirements.

Fishery biologists have devoted much effort in determining changes in fish populations as they respond to varying degrees of fishing intensity. Because stocks usually cannot be observed and measured directly, it has been necessary to use data of catch and fishing effort and biological data on relatively small samples of the stocks. These records, plus associated data on the environment, have composed most of the working materials of the fishery biologist. Limited to such materials, the fishery biologist has been forced to proceed largely by inference. There has been no alternative. As work became quantitative, inference came to mean statistical or biometric inference, or a combination of both.

One method of quantitative inference is that of simulation or modeling. Using the best empirical data and biological judgment available, the biologist erects hypotheses concerning the additive and subtractive processes affecting the stocks. The former include recruitment, growth, and immigration; the latter, fishing mortality, natural mortality, and emigration. To test the validity of the hypotheses, characteristics of the models based on the hypotheses can be compared with what is known of the real populations. Population models are used for the same purpose as models in ship or power-dam design: experiments are easier, quicker, and cheaper with the model than with the full-scale object. Any tool that will help the biologist in these processes should be valuable. This report describes such a tool in the form of an analog computer technique.

Application of the analog computer as described herein has not, to the best of my knowledge, been made previously. Originality is not claimed, however, for the technique of simulation in general or in

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

the field of fisheries. Familiar applications outside the field of biology include aircraft and spacecraft design, ballistic studies for military services, and management of systems such as power-generating pools and nuclear reactors. Among biologists, the ecologists especially have made use of simulation. Notable examples include the simulation of ecological systems by digital computer (Garfinkel and Sack, 1964) and by analog devices (Odum, 1960 and Margalef, 1962). In fisheries there have been three general types of simulation: analytical, digital, and analog.

Analytical simulation is the oldest and best known. It is so well known that an extensive review is superfluous here. In it the biologist analytically determines the nature of the mathematical relations controlling population structure and population response to exploitation. He then constructs mathematical models which predict what will occur under certain assumed conditions of the fishery and the environment. Most of the classical contributions to fishery dynamics are of this type. They include the work of such authors as Baranov (1918), Russell (1931), Thompson and Bell (1934), Graham (1935), Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). During the history of the analytical technique the complexity and sophistication of the formulations have generally increased; the work of Beverton and Holt unquestionably represents the highest development in this respect to date.

Some of the above authors have also used digital simulation. Thompson and Bell (1934) arithmetically constructed tables to simulate the catch and catch per unit of effort of the Pacific halibut under constant recruitment and certain assumed rates of growth and mortality. They demonstrated a remarkable correspondence between the values predicted by this method and the observed values for certain periods and areas. Ricker (1958) made somewhat similar calculations based on analytical functions and introduced the additional concept of relation between stock size and rate of recruitment. He expressed catches in terms of "equilibrium yields" which would be obtained when the additive processes affecting the populations just balanced the subtractive ones. An outstanding example of digital simulation of a fish stock is found in Larkin and Hourston (1964).

To my knowledge, only Doi (1957, 1962) has proposed application of the analog computer to fishery dynamics. He set forth mathematical formulations and computer block diagrams and made applications to Japanese fisheries. His formulas are similar to those used here, in general, but differ in detail. He also adapted the Volterra equations to analog treatment of predatory and competitive relations among fish populations.

With some notable exceptions (Ricker, 1958; Larkin and Hourston, 1964; Larkin and Ricker, 1964; International North Pacific Fisheries Commission, 1962), fishery-simulation attempts to date have dealt with equilibrium population conditions. This restriction is understandable in view of the mathematical complexities introduced by varying rates. Such an approach does, however, lead to models which are somewhat unreal compared with their counterparts in nature. For instance the number of recruits annually entering the stocks varies widely. This problem has been treated by considering recruitment constant for short periods (apparently close to the truth for some Pacific halibut stocks during various 8- to 10-year periods between 1918 and 1933) or circumvented by expressing results in terms of "yield per recruit." Likewise, fishing mortality varies with fishing intensity. Any realistic simulation of fished populations over considerable periods requires some provision for changes in recruitment and other vital rates, as can be accomplished on the analog computer. The importance of this problem was recognized by Schaefer and Beverton (1963) who wrote:

> ". . . . the characteristics of the recruitment to marine fish populations—its degree of fluctuation, its relation to stock size and the influence on it of changing environmental conditions—are the key to the interpretation and prediction of the long-term dynamics of a fishery . . ."

and:

> "Actual fisheries are, however, seldom in steady states . . ."

The remainder of this report is devoted to a description of the plan of attack (Platt, 1964—strong inference) used in the analog computer approach. Briefly outlined, this plan is as follows:

1. Formulation of vital rates in a manner suitable for analog solution, thus setting up a hypothesis.
2. Simulation of populations and yields over the period for which observational data are available.
3. Comparison of simulated and observed yields, testing the hypothesis.

4. Acceptance or rejection of the hypothesis. If the agreement of simulated with observed yields is good, the hypothesis is accepted. If it is rejected, a new hypothesis is erected by adjustment of parameters in the analog model, and steps 2 to 4 are repeated until satisfactory fit of simulated to actual yields is either attained or found unattainable.

In practice, the process was never repeated more than a few times, since improvement fell off rapidly. Also, indefinite repetition would be out of keeping with the scientific method.

BASIC FORMULATIONS

For the initial trials of the analog technique, I adopted what seemed the simplest useful model of a fish population. This model includes rate of growth, rates of fishing and natural mortality, and a recruitment-stock relation. It does not take account of immigration, emigration, or environmental effects. Symbols used have been adapted from Holt, Gulland, Taylor and Kurita (1959) in furtherance of their admirable attempt to secure uniformity in the terminology of fishery dynamics. Definitions are as follows:

N_t = Number of recruits surviving at time t.
R = Initial number of recruits to fishable stock for a single year class.
f = Fishing effort.
F = Instantaneous rate of fishing mortality.
q = F/f.
M = Instantaneous rate of natural mortality.
Z = $F + M$.
t = Age of fish in years.
t_r = Age of fish at recruitment to fishable stock.
t_c = Age of fish when first vulnerable to capture by gear in use.
P_t = Weight of all fish of a given year class surviving at time t.
P_{t_0} = Weight of all fish present at beginning of season.
w_t = Weight of individual fish at time t.
w_∞ = Upper asymptotic limit of w_t.
w_r = Weight of individual recruit at time t_r.
$\hat{Y}_w$ = Estimated yield of fishable stock in weight, per year.
Y_w = Actual yield of fishable stock in weight, per year, from official statistics.
E = Rate of exploitation, $= \dfrac{F}{F+M}\left(1 - e^{-(F+M)}\right)$.
i = Subscript referring to individual year classes.

In addition to the above, the following symbols have been adopted for the formulations here:

R_w = Initial weight of recruits to fishable stock for a single year class.
G, g = Constants of Gompertz growth curve.

Because interest in this study is centered on the commercial catch, the model is limited to the fishable sizes and ages of fish. For a year class of fish passing through the fishable stock, numbers of fish surviving may be expressed according to the declining exponential formula, as set forth in Beverton and Holt (1957):

$$N_t = Re^{-(F+M)\,(t-t_r)} \tag{1}$$

To take account of the growth of individual fish, and to obtain yields in weight for comparison with commercial catches, it is necessary to introduce a formula for weight-at-age. Beverton and Holt employed the von Bertalanffy equation for length-at-age, converting to weight-at-age by means of a cubic length-weight relation. Use of the cubic relation has been shown to lead to considerable error when the real relation between length and weight involves a power of length other than 3 (Paulik and Gales, 1964). Although this difficulty can be overcome by use of the Incomplete Beta Function (Wilimovsky and Wicklund, 1963) in the yield equation, the formulation still is not well adapted to analog computation.

As an alternative to the von Bertalanffy equation, I investigated the characteristics of the equation developed by Benjamin Gompertz. He applied it as an expression of human mortality rates, but various forms of it have since been used as growth curves for both length and weight of animals. Its applicability in this respect was thoroughly discussed by Winsor (1932). In the form used by Weymouth and McMillin (1931), it is seen to be an exponential curve in which the slope declines exponentially. They point out that the *relative* (as opposed to *absolute*) growth of an animal declines with age because of an increasing proportion of inactive material, and other causes. The declining slope of the Gompertz curve is in accord with this phenomenon. Also, it provided a good fit to the empirical data of weight-at-age for several fishes.

Beverton and Holt (1957) rejected the Gompertz curve on the basis that it deals with growth as an additive process only, ignoring the breakdown of protoplasm. The net effect, however, of anabolism and catabolism may well be the kind of declining relative growth described by the Gompertz curve. This curve thus did not appear to be rejected on biological grounds, and since it was practical for analog computation, I employed it.

It may be noted that growth rates of fish typically decline throughout life and can be represented most simply by a positive instantaneous rate which decreases exponentially with time, as in the Gompertz curve. The relations can be expressed in the following formulas (where G represents the initial exponential growth and g governs the exponential rate of decline):

$$w_t = w_r e^G e^{-Ge^{-g(t-t_r)}} \tag{2a}$$

$$w_t = w_r e^{G-Ge^{-g(t-t_r)}} \tag{2b}$$

This formula can be combined with formula (1) to express total weight of survivors at any time. It is of interest, also, that it has an upper asymptote w_∞ similar to the "L_∞" of the von Bertalanffy equation. Thus:

$$\text{as } t \longrightarrow \infty,\ e^{-g(t-t_r)} \longrightarrow 0$$

$$\text{and } e^{-Ge^{-g(t-t_r)}} \longrightarrow 1.00$$

so that $w_t \longrightarrow w_r e,^G$ as $t \longrightarrow \infty$ from equation (2a) above. The limiting value of this expression is w_∞. If extended from $w_t = 0$ to $w_t \sim w_\infty$, the Gompertz curve has a point of inflection lacking in the von Bertalanffy curve. This inflection is found in age-weight curves of many fishes. The total weight of survivors from a single year class may be expressed:

$$P_t = w_t N_t \tag{3}$$

Substituting in (3) for w_t and N_t their equivalents in (1) and (2b):

$$P_t = R w_r e^{[G-Ge^{-g(t-t_r)}]-(F+M)(t-t_r)}$$

Because I dealt with weight rather than number of recruits, I set

$$R_w = R w_r$$

and obtained as my working equation:

$$P_t = R_w e^{[G-Ge^{-g(t-t_r)}]-(F+M)(t-t_r)} \tag{4}$$

For convenience, clarity, and ready comparability with other work, I have dealt with all relationships so far in algebraic form. Although the computer requires differential equations, the differentiation can be performed on the final equation, (4) above.

THE COMPUTER AND PLOTTER

Since analog machines probably are not familiar to most fishery biologists, a brief description seems in order. Modern analog computers (fig. 1) are electronic and perform operations on voltages. The voltage is made numerically equal (analogous) to variables in the problem (e.g., 1 volt = age of fish of 2 years), and component building blocks on the computer perform mathematical operations. Various blocks perform: (1) algebraic summation, (2) multiplication or division by a constant, (3) multiplication and division of two variables, (4) integration, and (5) generation of nonlinear functions. This last building block makes it possible to produce functions if a graph of the function is available even though the equations describing the graph are unknown.

The analog computer is primarily a device for solving differential equations with time as the independent variable. It, therefore, becomes evident that if a biological process can be expressed as a differential equation, the equation can be mechanized by interconnecting analog computer components corresponding to the mathematical operations.

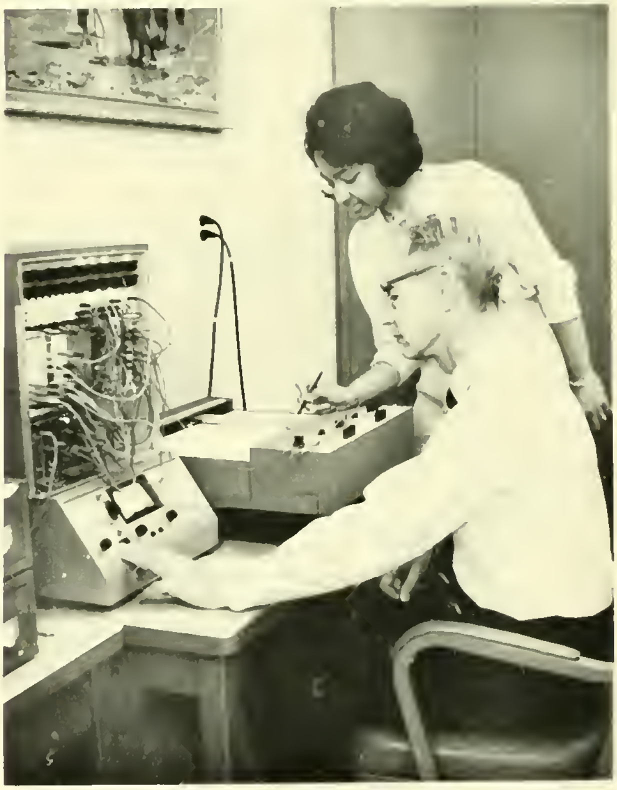


Figure 1.—Analog computer and plotter.

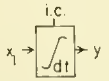
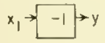
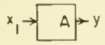
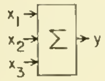
Analog computer programming is based essentially on the electrical principle of the feedback loop. For a simple illustration, let us return to the declining exponential curve, as expressed in equation (1). This expression may be further simplified by setting $F+M=Z$, as in international notation and assuming that our measurement of time begins at t_r so that $t_r=0$ and $(t-t_r)=t$. Expression (1) then becomes:

$$N_t=Re^{-Zt}$$

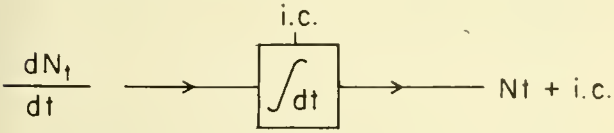
Remembering that the analog computer requires differential expressions, we differentiate the above to find:

$$\frac{dN_t}{dt}=-RZe^{-Zt}$$

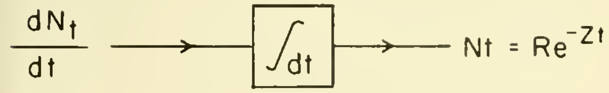
As in digital computation, we start with a "block diagram" (ordinarily this step would be omitted in such a simple circuit, but it is shown here to illustrate the process). A few symbols are needed (arrows indicate direction of information flow):

OPERATION PERFORMED BY COMPUTER	SYMBOL	EQUATION
Integration with respect to time		$y=\int_0^t x_1\,dt + i.c.$ $i.c.=y]_{t=0}$
Inversion (Change of sign)		$y=-x_1$
Multiplication by a constant		$y=Ax_1$
Summation		$y=x_1+x_2+x_3$

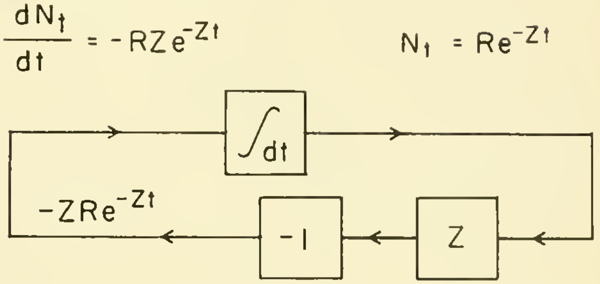
Using the first three of these symbols, we can now construct a block diagram for our differential expression. We start by assuming that a voltage proportional to dN_t/dt exists:



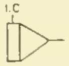
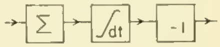
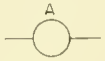
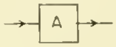
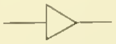
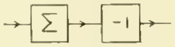
Considering only the rate at which N_t changes, and disregarding its absolute value, we can omit the constant of integration (this constant will be added in the circuit diagram):



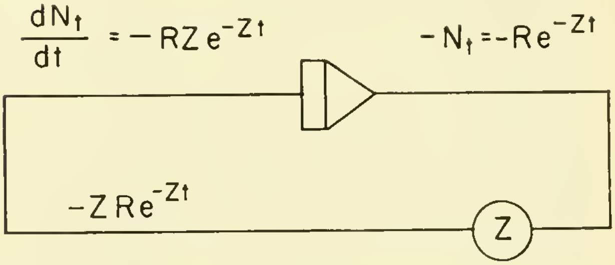
But we know that $\frac{dN_t}{dt}=-RZe^{-Zt}$, so we simply assemble the derivative:

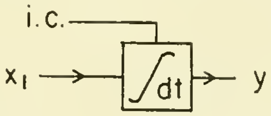


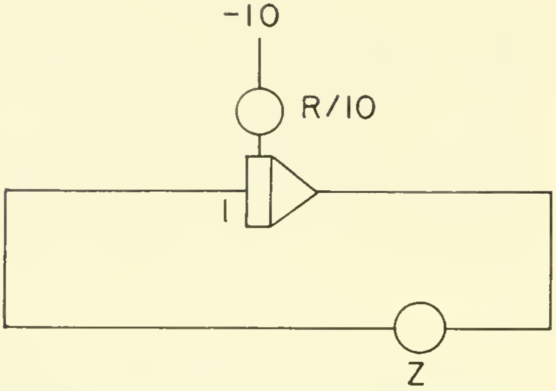
The next step is to construct a circuit diagram showing the actual computing elements and taking account of "initial conditions" and any sign changes that may occur. For this step we use additional symbols:

COMPUTING ELEMENT	SYMBOL	BLOCK DIAGRAM EQUIVALENT
Integrating network with Summing Junction		
Potentiometer		
Summing amplifier		

Still disregarding *i. c.*, we have:



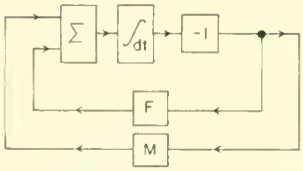
Finally we must supply the "initial condition" voltage, *i.c.*, which is equal to the constant of integration. We noted above, in the definition of the symbol  that $y=\int_0^t x_1 dt+$ *i.c.* and $i.c.=y]_{t=0}$. In our equation "y" is replaced by N_t. Since we set $t_r=0$, by definition $N_t]_{t=0}=R=$ *i.c.* The completed diagram, assuming a computer reference voltage supply of −10 volts, becomes:



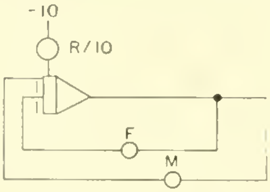
In the operation of the integrating network, *i.c.* only determines the value of N_t (condenser charge) at the beginning of the computation. It is cut off the instant computation begins, and current flow is then confined to the feedback loop. That is why *i.c.* does not appear as a variable in the block diagram. The figure "1" by the integrator input refers to the input resistor. Operation of the integrator is such that the input is multiplied by a factor $100/R_t$ when R_t = input resistance in kilohms.

With the knowledge now at hand we can proceed to set up a circuit in which Z is divided into its components F and M. The equation becomes $N_t = Re^{-(F+M)t}$ and the diagrams are:

BLOCK DIAGRAM



CIRCUIT DIAGRAM



Study of the circuit used here (fig. 2) reveals it to be essentially an elaboration of the basic feedback loop. A multiplier has been added to take care of the nonlinear Gompertz growth curve, and other elements have been added as described in the text. The "time-base" (t) is generated by a simple integrator output. Biologists interested in further information on analog computer programming will find an excellent brief introduction in Strong and Hannauer (1962) or a more extended treatment in Ashley (1963).

The plotter has a pen actuated by two servomotors. One moves it along the "X" axis and the other along the "Y" axis in proportion to an input voltage supplied by the computer. Thus the pen moves to any point X, Y in a system of rectangular coordinates on the plotting surface, corresponding to input voltages V_x and V_y. Since the computer integrates with respect to time, a voltage directly proportional to time is usually fed into "X." The input for "Y" can be taken from any point on the computer circuit to plot the variable(s) desired against time.

As an alternative method of output display, an oscilloscope can be used. This combination requires that the computer be modified for "repetitive operation." Problem solutions are repeated 10 to 100 times per second, so that they appear as curves on the oscilloscope screen. For a permanent record the screen can be photographed as mentioned by Doi (1962).

This oscilloscope display is particularly valuable for curve fitting, since points can be plotted on the face of the tube. In this manner the effect of the potentiometer adjustment in improving the fit is instantly seen.

The work described below was performed on a Pace TR–10 analog computer in conjunction with an EAI Variplotter 1110. The TR–10 is one of the smallest general-purpose analog machines. Since both computer and plotter are fully transistorized, they are small and can be used conveniently atop a desk or small table. The set of units available in the computer as I used it was as follows:

Unit	*Number*
Amplifier (used with integrator, multiplier, etc.)	10
Coefficient potentiometer (used as above)	18
Null potentiometer (used to set coefficient potentiometers)	1
Integrator (used as above)	4
Multiplier (used as above)	1
Diode function generator (use described later in text)	1
Comparator (use described later in text)	1

GENERATION OF SURVIVAL CURVES

The differential equation needed for generating the survival curve of a given weight of recruits, R_w, is obtained by differentiating expression (4):

$$\frac{dP_t}{dt} = R_w e^{[G - Ge^{-g(t-t_r)}] - (F+M)(t-t_r)} [gGe^{-g(t-t_r)} - F - M] \tag{5}$$

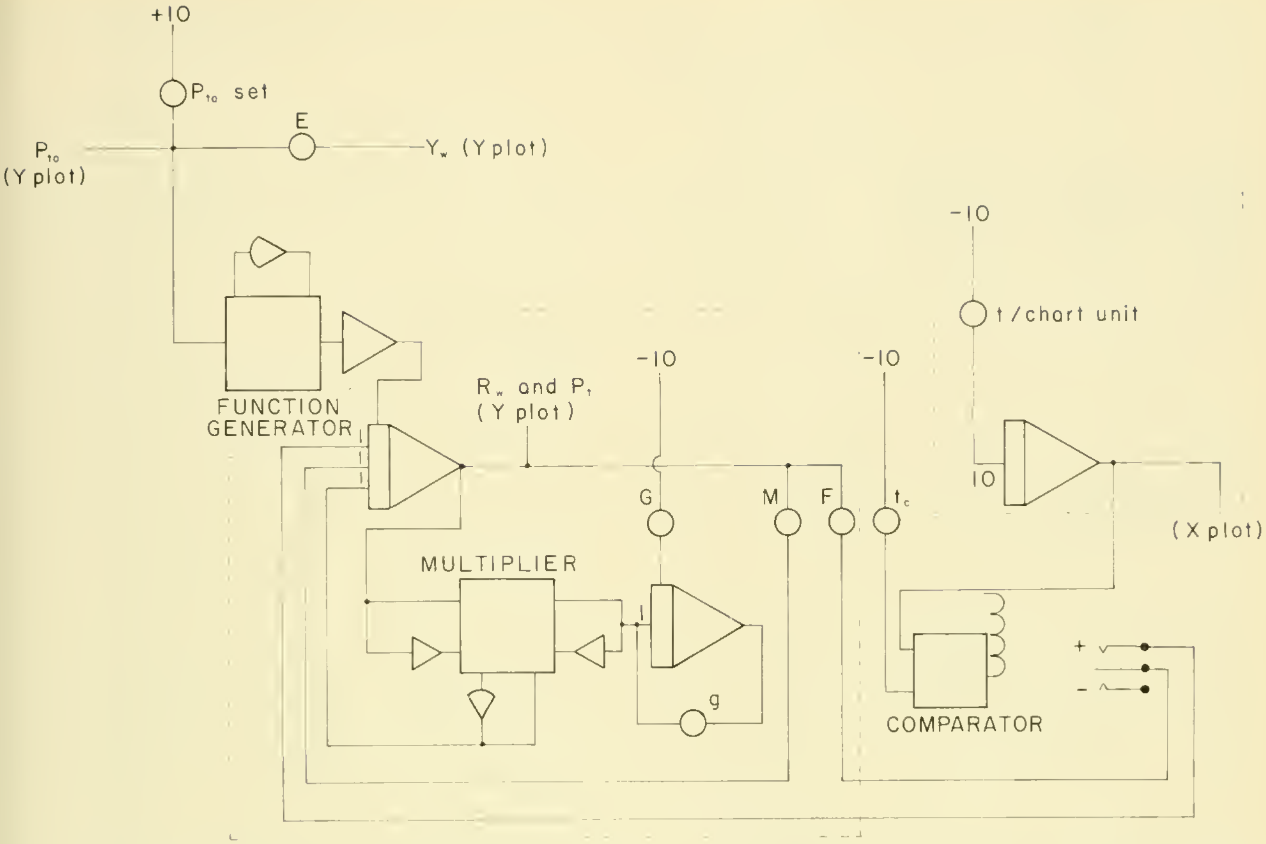


FIGURE 2.—Analog computer circuit for generation of P_t and Y_w. Standard symbols for computing elements, scaling excluded.

By integrating this expression, the computer generates P_t as a function of $(t-t_r)$ for any given values of R_w, g, G, F, and M. The circuit diagram, which includes conventional symbols for the computing elements, is shown within the broken line enclosures of figure 2. The elements outside the broken lines are used in the combination of analog and graphical computation employed to sum the weights of year classes for each season and to determine subsequent recruitment. Their nature and use are described later.

As examples of analog computation, growth and survival curves from the plotter are shown in figures 3 and 4. The data are hypothetical except for the growth constants, which have been derived from data for the California sardine.

Data of growth in weight were obtained by combining a curve of growth in length with a weight-length relation. A table of length-at-age was given in Phillips (1948) and a weight-length relation in Clark (1928). Fitting of the Gompertz relation to these data (fig. 3) was readily accomplished by successive trials, with appropriate adjustment of the potentiometers for G and g. The fitted curve followed expression (2b), with $w_r=93$ g., $G=0.825$, $g=0.445$, and $t_r=2$ years.

Starting with a hypothetical 1,000 fish, $R_w=93$ kg. when $w_r=93$ g. The upper curve (fig. 4) shows how, with no fishing mortality and low natural mortality, P_t may increase for a year or two before mortality overcomes growth. In the two lower curves the effect of adding a substantial fishing mortality may be seen. Application of an increase in fishing mortality at $t-t_r=2$ resulted in the lower branched curve. This change is readily made on the analog computer by placing the machine in the "hold" mode. The potentiometer for "F" is then reset, the machine returned to "operate" mode and the computation resumed. The ability to change quickly the vital rates during a computation is one of the advantages of the analog machine. It may be done even more conveniently by presetting a number of

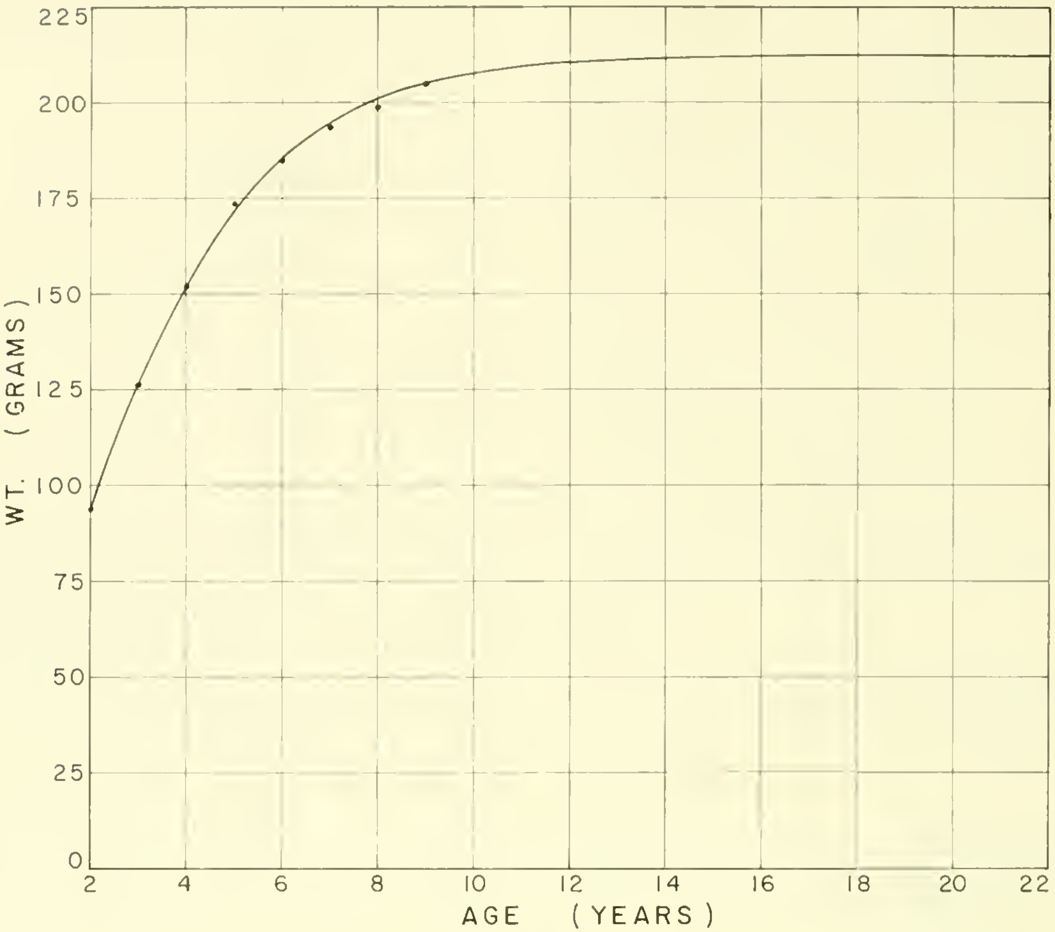


FIGURE 3.—The Gompertz curve fitted to weight-at-age data for the Pacific sardine following expression (2b) in text; $w_r = 93$ g., $G = 0.825$, $g = 0.445$, and $t_r = 2$ years.

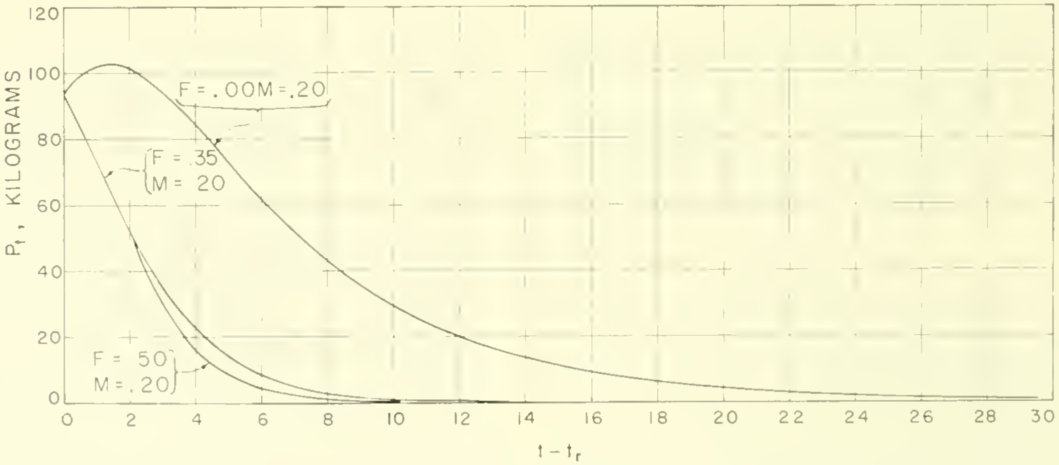


FIGURE 4.—Computer curves of P_t as a function of $(t\text{-}t_r)$; growth data from the California sardine, according to expression (4) in text. Values of constants are: $R = 1{,}000$ fish, $w_r = 93$ g., $R_w = 93$ kg., $G = 0.825$, $g = 0.445$.

potentiometers at needed values of "F" and shifting from one to the other.

PROCEDURE OF SIMULATION

Simulation of populations and yields by a combination analog-graphic approach required development of a standardized procedure. A chart was prepared for the plotter, with appropriately scaled coordinates for time (X-axis) and stock (Y-axis). Vertical lines on this chart marked the points for changes in mortality rates or recruitment relation.

Because the commercial stock in any fishing season is made up of survivors from individual year classes of various ages, that stock cannot be started "full blown," with all year classes present. I therefore started with a stock size such that the rate of exploitation (E) estimated to be in effect would produce a catch ($\hat{Y}_w$) equal to the real catch for the first fishing-season, or the mean catch for the first two fishing-seasons of the study period. This stock was then built up by starting year classes at times 1, 2, 3, . . . n years before the beginning of the period; n represents the number of years for a year class to pass through the fishery. During this "prestudy" period, the mortality rates in effect at the beginning of the study period were assumed to be in effect. Each ith curve begins at the value of R_w (assumed the same for each year class) required to produce the specified initial value of total stock $P_{to} = \sum_{i=1}^{i=n} P_{ti}$. This value of R_{wi} can be quickly determined by a few computer trials. P_t for each year class is generated until it declines to a small arbitrary value close to zero, but only the portion extending into the study period is plotted.

The initial and subsequent values of P_{to} are calculated by graphically summing the heights P_{ti} of the ith survival curves for each fishing season, by means of a pair of dividers. Once the initial value of P_{to} has been obtained, the calculation is self-sustaining. From the recruitment curves, values of R_{wi} corresponding to P_{to} t_r years before are obtained. R_{wi} is generated as a function of P_{to} in the Diode Function Generator (fig. 2) by the simple device of setting the P_{to} potentiometer so that the plotter "Y value" corresponds to the P_{to} value for the particular year in question. R_{wi} is then plotted by attaching the Y input to the R_w point in the computer circuit. Any empirical or theoretical curve relating recruitment to spawning stock can be set into the Diode Function Generator, which, with an input x_1, produces an output in the form of a curve $y = f(x_1)$, composed of 10 straight segments.

Survival curves as described above can be generated for each year class entering the fishery during the study period. As in the case of the initial season just described, heights P_{ti} of the individual survival curves for each year are summed graphically, and a mark made representing the total commercial stock, $P_{to} = \sum_{i=o}^{i=n} P_{ti}$. The "$P_{to}$ set" potentiometer is adjusted to bring the "Y-value" of the plotter into conformance with the total stock value P_{to}. The catch is calculated by setting potentiometer "E" (Fig. 2) at the value $E = \frac{F}{F+M}[1 - e^{-(F+M)}]$. The catch or yield value proceeds from the simple relation $\hat{Y}_w = EP_{to}$. It is plotted by attaching the "Y input" of the plotter at the point Y_w in the computer. After plotting of $\hat{Y}_w$ the process for R_{wi} (above) is repeated, and the cycle recommenced.

In outline, then, the process of simulating population and yield is as follows:

1. Set the initial value of $\hat{Y}_w$ at the size of the actual catch for the initial year or two of the study period.
2. Determine initial $P_{to} = \sum_{i=o}^{i=n} P_{ti}$ from the relation $P_{to} = \hat{Y}_w / E$.
3. By computer trial, find value R_{wi} such that $\sum_{i=o}^{i=n} P_{ti} = \text{initial } P_{to}$.
4. Generate n curves of P_{ti}, where n is the number of years required for P_{ti} to decline from R_{wi} to an arbitrary small value near zero. Start at 1, 2, 3, . . . n years before the beginning of the study period.
5. By Diode Function Generator evaluate R_{wi} for each season from P_{to} for season t_r years before. Generate curves P_{ti} starting at $P_{ti} = R_{wi}$ for each fishing season.
6. For each fishing season, graphically determine $P_{to} = \sum_{i=1}^{i=n} P_{ti}$. Calculate $\hat{Y}_w = EP_{to}$.

7. Repeat cycle to end of study period, starting each cycle with step No. 5.

EXAMPLE OF APPLICATION

Since hypothetical data are seldom satisfactory to demonstrate the application of a technique, the following example of application to the fishery for Atlantic cod (*Gadus morhua*) is included. It has been used to achieve concreteness, not to make new discoveries about the cod. Catch data were summed for International Commission for the Northwest Atlantic Fisheries Divisions 5Y and 5Z, and the following parameters were assembled for analog computation:

1. The central value of $F=0.35$ used in Beverton and Hodder (1962) was assumed to be the average ($\bar{F}$) for the entire study period 1932–1958. From this figure, values were calculated for eight periods, from the relation $F=qf$, where f was value of fishing effort from Beverton and Hodder and $q=\bar{F}/\bar{f}$:

Period	Mean effort thousands of boat-days	$F=qf$, holding mean $Z=0.55$ for:	
		$M=0.2$ (Trials 1 and 2)	$M=0.25$ (Trial 3)
1932–33	2.00	0.36	0.31
1934–36	1.13	.20	.18
1937–38	2.00	.36	.31
1939–41	2.77	.50	.43
1942 only	1.80	.32	.28
1943–46	1.22	.22	.19
1947–48	1.80	.32	.28
1949–58	2.24	.40	.35

2. The central value $M=0.2$ given by Beverton and Hodder was assumed to be in effect during the entire study period.
3. Lengths-at-age were o[illegible]ed from Schroeder (1930) and convert[illegible]ights-at-age with a length-weight cu[illegible] to data given in Bigelow and Schroeder (1953). A Gompertz curve was fitted to the weights-at-age with constants $G=1.47$, $g=0.340$, and $w_r=5.9$ lb.
4. No empirical data were available as the basis of a stock-recruitment curve. After some preliminary experimentation, a hypothetical curve (fig. 5A), with mode at an arbitrary $R_{wt}=32{,}000$ metric tons, was adopted for the first formal trial. The concavity of the left hand limb was based only on experience from other species. From data on age composition in Beverton and Hodder it was estimated that $t_r=4$ years.
5. From data in Beverton and Hodder (1962) and Silliman and Wise (1961), it was estimated that if $t_c=t_r$ before the change in cod-end mesh size from $2\frac{7}{8}$ to $4\frac{1}{2}$ inches in 1954, then $t_c=t_r+0.25$ year for 1954 and thereafter. This change was accomplished by the comparator (fig. 2), a device which actuates a switch when the input (t in this application) reaches a predetermined value (t_c here). The comparator delayed application of F for one quarter of a year, for year classes entering in 1954–58.

The initial trial simulation, based on the parameters just listed, produced a poor fit of calculated ($\hat{Y}_w$) to actual (Y_w) catches ($r=-0.17$). On the basis of this trial, the shape of the recruitment curve was altered somewhat (fig. 5B) for the second trial. All other parameters remained the same. After the recruitment relation was revised, a second trial produced a considerably improved fit ($r=0.59$). Finally, the value of M was changed to 0.25 and mean F to

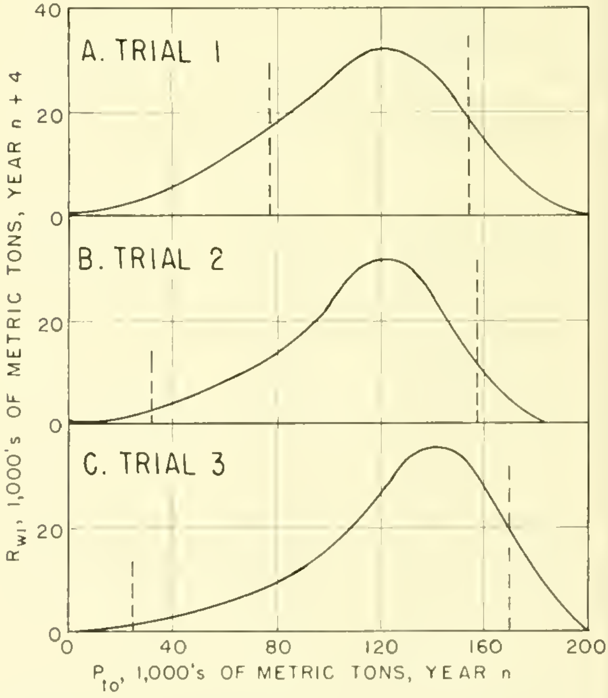


FIGURE 5.—Hypothetical recruitment curves for New England cod. Vertical broken lines indicate range of values used in computations.

0.30, so that $F+M$ remained 0.55. A further adjustment was also made in the recruitment curve (fig. 5C). The third trial, in which these adjustments were employed, yielded a further improvement in the fit ($r=0.69$), which is shown in figure 6. A notable feature of the trials was the sensitivity of the fits to changes in the stock-recruitment relation. The greatest improvement in fit occurred between the first two trials, as the result solely of a moderate change in the shape of the recruit curve (figs. 5A, 5B).

The series $\hat{Y}_w$ and Y_w are not, of course, completely independent, since Y_w enters to some extent into the calculation of the parameters used to compute $\hat{Y}_w$. As a relative measure of goodness of fit, however, the coefficient is of some value. It is possible to make at least two positive statements regarding r as used here:

1. If the calculated P value is greater than the significance level, the real value is certainly greater. Additional degrees of freedom will be lost according to the degree of dependence of the variables. It is possible, then, to identify markedly nonsignificant fits.
2. For calculated correlations within conventional significance levels, the value of r serves as a means of comparing two fits. If one set of parameters generates a fit with a higher value of r than another, then it should be closer to the truth than the other.

The parameters used in the simulations have varying and subtle degrees of dependency on the catch data. Thus, to assess accurately the value of P for the coefficients would require a lengthy and complicated statistical analysis. This work appears hardly to be warranted in view of the approximate nature of the simulations.

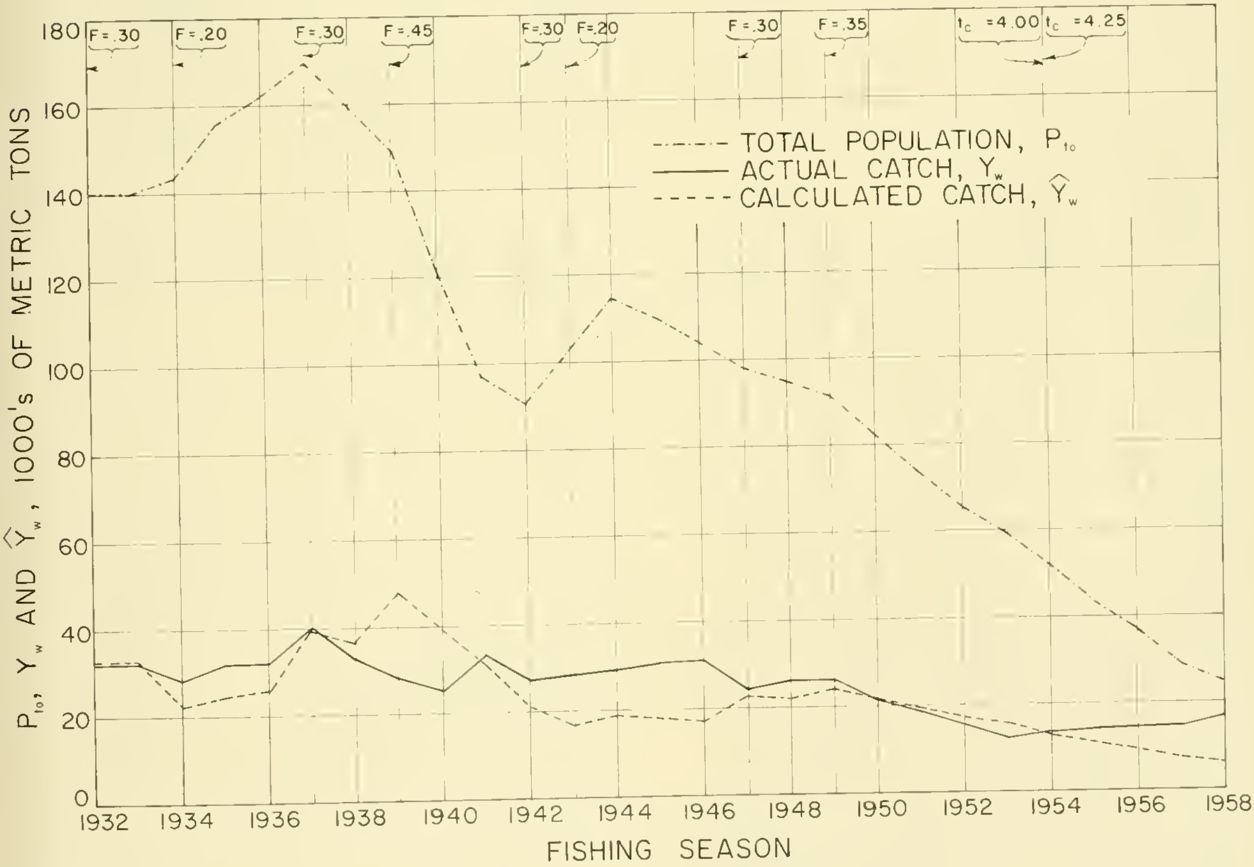


FIGURE 6.—Population and yield simulation for New England cod; $M = 0.25$, $G = 1.47$, and $g = 0.34$ for entire period. Other parameters as shown in drawing.

GENERAL APPLICATION OF THE TECHNIQUE

Application of the analog computer technique described in this report requires estimation of a series of constants or parameters. It also requires a number of approximations and some appraisal of their uniqueness. These two topics will be discussed in this section.

PRELIMINARY ESTIMATES OF PARAMETERS

An extensive literature is available on the estimation of parameters of fish populations under exploitation. The most thoroughgoing summaries and descriptions known to me are given in Beverton and Holt (1957) and Ricker (1958). Treatment here is limited to the specific constants, variables, and relations which must be estimated for simulations by analog computer as described above. They will be considered in descending order of the degree of certainty with which they are likely to be known.

1. Annual yield. For most commercial fisheries this figure is likely to be known rather precisely. Since the original data come from weighouts at the time the fish are first sold, their accuracy has been watched closely by both fishermen and fish buyers. If possible, catches should be segregated according to biological stock units.

2. Growth in weight. Lengths or weights at specific ages are among the most commonly gathered fishery data. If data are in lengths, they must be converted to weights through a length-weight curve. The length-weight relation is fairly stable as compared with other parameters and can be determined from a relatively small number of samples covering the size range of the fish in question. The Gompertz growth curve can be fitted to the empirical data directly on the analog computer simply by adjusting potentiometer settings for G and g until a good fit is obtained.

3. Instantaneous fishing mortality rate, F. This rate may be difficult to estimate with accuracy. If empirical estimates are lacking, however, it may be possible to produce an "educated guess" through general knowledge of the history of the fishery, its changes in yield, the size of the current fishery, ... This value can be adjusted during simulation.

Once a value of F is available for one period, the values for other periods can be estimated if fishing intensity is known. Data on the number and size of units in the fleet are usually available. These figures must be multiplied by an estimate of time in operation to obtain the value of fishing effort, f. Once a series of values of f is on hand, together with F and f for a "base period," values of F for all periods can be calculated from the relation $F=qf$, where q is a constant to be determined from the base-period data.

4. Instantaneous natural mortality rate, M. Estimates of M may be available from tagging or biological data, or an assumed value may be selected for the initial trial. If an assumed value must be used, guidance can often be obtained from the growth characteristics of the fish (Beverton and Holt, 1959; Beverton, 1963). For fish in the commercially available stock, values of M are often low, in the vicinity of 0.1 to 0.3. Frequently, reasonable approximations can be obtained by considering M to be constant during the study period, for all ages of fish.

5. Stock-recruitment relation. Of the items required for simulation, this one is usually the most difficult to obtain. If data are available on age composition, it may be possible to estimate the abundance of the youngest (or youngest important) year class in the commercially available stock. A series of such estimates can then be related to the estimated size of the spawning stock t_r years earlier, as was done by Clark and Marr (1955). The resulting scatter diagram may reveal a pattern that can form the basis for one or more recruitment curves. It is significant that only the portion of the curve covering the stock sizes encountered can affect the outcome of the simulation.

SUCCESSIVE APPROXIMATIONS AND UNIQUENESS

Once the preliminary estimates of the parameters are assembled, simulation trials can begin. Because all the work is visible on the computer chart as it proceeds, it is often possible to see in what direction the parameters must be changed to produce a better fit of calculated to actual catches. Experimentation is readily accomplished, since all parameters may be changed simply by resetting potentiometers (either coefficient potentiometers or the several small ones in the Diode Function Generator). For trials in the applications above, each trial for 26 or 27 fishing seasons consumed about one-half day. This work included preparation of the chart and all other necessary operations leading to a plot of annual populations and yields. It is thus possible to accomplish several trials within a reasonable period of time.

In any trial-and-error approach involving several variables, the question of uniqueness must be faced. It is fair to ask, if one set of parameters has produced a reasonable result, may not another set produce one that is equally reasonable?

Although it is not possible to answer the above question for the general case, some light may appear from a further examination of the trials on cod reported above. In assessing goodness of fit, I took account of the ratio of mean heights of the calculated and actual catch curves, as well as the correlation between them. Thus I had two criteria of "goodness of fit": $\bar{\hat{Y}}_w/\bar{Y}_w$ and r. To provide some idea of the discriminative value of these criteria, I made additional simulations in which only F or M was varied and all other parameters were held constant. Curves of calculated values (fig. 7), bracketing those used in the third trial above, are revealing. For this particular set of combinations, only one other than the third approaches its "goodness of fit." The combination of $F=0.35$ with $M=0.25$ produced about as good a fit as the combination of the third trial; r was slightly higher, and $\bar{\hat{Y}}_w/\bar{Y}_w$ was slightly lower. The difference in F of 0.05, however, is well within what might be considered reasonable error in a rough approximation.

Obviously, curves of the type in figure 7 cannot "prove" the uniqueness of fit obtained with any particular combination of parameters. Since F, M, and the shape and height of the recruitment curve can be continuously varied, the number of possible combinations is infinite. Every effort should be made, therefore, to use reasonable values of biological parameters. Thus we know that F, M, and the recruitment curve are sound because biologists generally recognize that fish stocks are affected by fishing, natural mortality, and recruitment. The question of "reasonable values" is more difficult, but the range of possibilities may be narrowed by use of empirical data as indicated under "Preliminary Estimates of Parameters."

COMPARISON WITH OTHER TECHNIQUES

By appropriate transformations of the formulas, any of the calculations reported above can be performed on either conventional desk calculators or electronic digital computers. It is pertinent, therefore, to consider the relative advantages and disadvantages of analog computation as compared with other techniques.

1. *Initial cost of equipment.*—The analog computer and plotter equipped as I used them cost about $8,000. This figure is substantially more than a good desk calculator ($1,000 to $2,000) but not over one-tenth the cost of comparable digital equip-

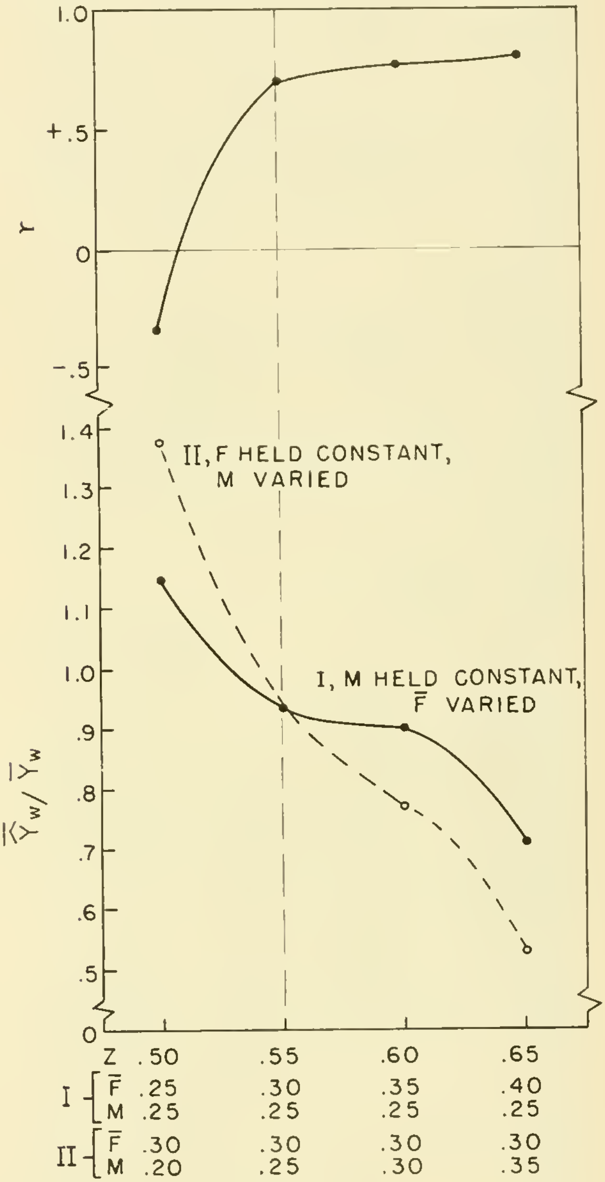


FIGURE 7.—Effect of varying F or M in simulation trials with cod. The value r is the coefficient of correlation between calculated catches ($\hat{Y}_w$) and actual catches (Y_w). Since r is affected only by Z, and not the ratio of its components F and M, it has only one value for each pair of combinations. The fraction $\bar{\hat{Y}}_w/\bar{Y}_w$ represents the ratio of the mean calculated catch ($\bar{\hat{Y}}_w$) to the mean actual catch ($\bar{Y}_w$). Vertical line of dashes indicates combination of values used in third cod simulation trial.

ment. It is, of course, possible to perform work on digital machines under contract or rental arrangements at no initial cost. This arrangement is also possible for analog machines.

2. *Time required for computation.*—For the total operation as outlined above, limited tests indicated analog-graphic computation to be about four times as fast as desk calculation. With digital computers, the calculation time is a matter of minutes. If time required for preparation of data for computer calculation, programming the computer, and exchange of data with the computer center are considered, however, total time may well approach that for the analog method.

3. *Visibility of work during computation.*—In the analog-graphic method, stock size, recruitment rate, and yield are all visible in graphic form as the computation proceeds. This advantage is important to the biologist, since it quickly reveals absurd results, or permits him to end a computation that is leading away from reality. Work is invisible during digital computation, and the final "readout" is usually in the form of a table that may have to be plotted for study.

4. *Scale adjustment.*—Quantities generated within an analog computer must be kept within the voltage limits of the machine. This limitation leads to a considerable amount of "fussing" to achieve proper scaling of the variables. This problem is only minor in digital calculation and therefore represents a comparative disadvantage for the analog computer. Fortunately, once scaling has been adopted for a given formula, it can usually be used with only one or two changes when shifting to a new set of empirical data for the same formula.

5. *Accuracy of results.*—Because of the nature of components in an analog computer, the final results are usually accurate only to two or three significant digits. At the present stage of development of fishery science, the empirical data available are not such as to justify carrying more digits. In fact, two-digit accuracy in fishery predictions would be considered more than satisfactory by most fishery administrators. Thus, the accuracy limitations of the analog machine as compared with digital computation do not at present represent a serious disadvantage.

6. *Summary comparison of methods.*—From the above brief listing, the analog technique is seen to have advantages in comparatively low initial cost of equipment, moderately rapid computation rate, and visibility of results. It has limitations in accuracy and in scaling requirements and is slower than a digital computer. Decision as to which technique to use must depend on the situation of the individual investigator. Factors bearing on the decision include the salaries of persons doing various parts of the work, the accessibility of the research station to a digital computer, and the types of empirical data available.

UTILITY OF THE TECHNIQUE

In this report I have described what may be a useful working tool for the fishery biologist. The example of application given demonstrated the types of basic data needed and the way in which they could be adjusted to improve "goodness of fit" of calculated to actual catches. As with any technique, its utility can be assessed only by those making use of it.

Where extensive biological data are available, simulation is valuable in determining the effects of interaction among the varying mortality, growth, and recruitment rates. The accuracy with which actual catches can be reproduced should serve as a check on the validity of the sampling, analysis, and interpretation involved in the derivation of population parameters.

SUMMARY

1. The objective of this study was to develop an analog-computer simulation technique for modeling exploited fish populations.

2. The mathematical formula for survival of a year class expressed the effect of fishing and natural mortality rates and incorporated a Gompertz curve of growth.

3. Survival curves for successive year classes were generated on an analog computer through use of the differential form of the survival formula. A combined analog-graphic technique summed the weights of survivors in each season to give the weight of the fishable stock.

4. Yield was calculated by applying the rate of exploitation to the fishable stock.

5. Properly lagged recruitment was determined from the stock weight through a stock-recruitment curve.

6. Mechanics of the technique were demonstrated by application to the Atlantic cod.

7. This technique may be applied to any fishery for which good measures or estimates of catch,

growth rate, fishing and natural mortality, and stock-recruitment relation can be obtained.

8. The problem of uniqueness was studied from simulations in which F and M were varied over a range of values. The failure of results to prove uniqueness brings out the importance of using reasonable values of parameters.

9. As compared with other techniques, the analog-graphic approach described here offers low initial cost of equipment, moderate computation speed, ready accessibility of equipment, and good visibility of results during computation. It has limitations in accuracy (two or three digits) and in requirements for scaling variables.

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A SEROLOGICALLY DETECTED SERUM FACTOR ASSOCIATED WITH MATURITY IN ENGLISH SOLE, *PAROPHRYS VETULUS,* AND PACIFIC HALIBUT, *HIPPOGLOSSUS STENOLEPIS*[1]

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ABSTRACT

An antigenic serum component in maturing female pleuronectids was detected by immunodiffusion techniques. Its presence was related to age, length, and maturity in English sole (*Parophrys vetulus*) and Pacific halibut (*Hippoglossus stenolepis*). The factor had a qualitative seasonal variation for English sole; the highest incidence was during the spawning season and the lowest at midsummer. The factor was detected in all mature female halibut sampled, but complete seasonal data are lacking for this species because samples were not available in summer and fall. The factor was detected in the serum of some immature females of both species during the spawning season. Evidence associating the synthesis of this factor with the production of estrogenic hormones was obtained when estradiol was injected into male English sole and induced them to produce the factor.

Maturity studies are an important aspect of biological investigations of fish. Knowledge of age and size at maturity, fecundity, and duration and frequency of spawning is generally required in the management of a species. As a result of the importance of information on maturity, a wealth of literature exists on the subject covering a broad range of fish species. Most maturity investigations have been concerned with development of ovaries rather than testes because of the importance of egg production in population dynamics.

Biological studies of maturity of the Pleuronectidae (flounders) are representative of the variety of approaches for fish generally. Pleuronectid ovaries may be easily classified as developing or immature by macroscopic inspection during the intervals before and after (and including) the spawning season. Harry (1959) used this method to study time of spawning, length at maturity, and fecundity in three species of flounders. Use of a maturity scale, devised by Heincke (1898) for North Sea herring investigations, allows more quantitative estimates of annual ovarian variations. To calculate the spawning season of the Dover sole (*Microstomus pacificus*) Hagerman (1952) used a typical modification of Heincke's scale, based on grossly discernible criteria such as size, transparency, and presence of macroscopic ova. More precise information can be gained by examining the interior of the ovary. By microscopic study of egg diameter and the development of ova, Thompson (1915) determined the presence of egg stocks for more than one season in the Pacific halibut (*Hippoglossus stenolepis*) and found an extended spawning interval for individual females. Through histological methods, Franz (1910) identified four distinct developmental stages and established a firmer understanding of the maturity process than could be done solely by external observations of the ovary in plaice (*Pleuronectes platessa*).

Characteristic changes in the blood of certain

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[1] This material was included in a thesis submitted by Mr Utter in partial fulfillment of the requirements for the M.S. degree from the Graduate School of the University of Washington

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Note—Approved for publication September 21, 1965.

female vertebrates are related to maturity and can be studied by biochemical and serological techniques. Serum vitellin has been associated with maturation in hens (Roepke and Hughes, 1935) and related serologically to egg vitellin in fowl (Roepke and Bushnell, 1936). Analogous conditions have been described in other oviparous vertebrate classes including teleosts. Uhlenhuth and Kodama (1914), as quoted by Sasaki (1932), used antisera prepared from carp ovaries to distinguish serum of mature female carp from serum of immature female and male carp. Ridgway associated a serologically detected serum factor of the sockeye salmon (also found at high concentrations in the egg) with maturity in females (Ridgway, Klontz, and Matsumoto, 1962); subsequently he has found the antiserum to cross-react with mature females in all salmonid species tested (Ridgway, unpublished data). Concurrently, Vanstone and Ho (1961), in studies of electrophoretic patterns of coho salmon sera at various stages of development, observed a component that was characteristic of maturing females. Fine and Drilhon (1963) identified a similar protein in *Salmo salar* by immunodiffusion. Existing evidence indicates that serum vitellin may be accounted for by the following sequence of events in oviparous vertebrates: under the control of the pituitary, estrogen produced in the ovary stimulates production by the liver of proteins that are passed through the blood to the ovary and there utilized in yolk formation.

The present study attempts to unite the biological and serological approaches in investigations of the maturity of two pleuronected species. We originally intended to study only Pacific halibut. When we found that collecting an adequate halibut sample was impractical, we included English sole (*Parophrys vetulus*), a more available species. The study is based on a serum-vitellin component, called the HM factor, which occurs in mature female flounders. The objective is to demonstrate that serological methods may be advantageously applied in maturity studies of these species by showing the relation of the factor to various biological features.

METHODS AND MATERIALS

The serological methods, preparation of the antigenic substance used in the methods, and the collection of samples for analysis as well as for determination of age of fish from which samples were taken are described.

SEROLOGICAL METHODS

The procedure for the detection of the HM factor was a microslide adaptation of the Ouchterlony method of double-diffusion precipitin analysis as described by Ridgway et al. (1962). The diffusion method provides a means of identifying antigenic components of a solution through diffusion of the solution and an antiserum towards one another in a semisolid medium.[3] If the antiserum contains antibodies specific for components of the solution, a precipitate line is formed in the zone where given antigen molecules meet specific antibodies in optimal proportions. If two antigen solutions that are placed adjacently diffuse towards a single antiserum source, precipitate lines for common antigen-antibody systems will fuse.

Tests for the presence of the HM factor were made in the manner illustrated in figure 1. Sera from known HM-positive females were placed in positions 1 and 4, thus placing each unknown serum adjacent to an HM-positive individual. Distinct positive reactions are seen in positions 5 and 6; a weak positive reaction in position 2, and no reaction in position 3. This arrangement was particularly useful for positive individuals with low concentrations of HM antigen. Although a distinct line was not necessarily formed, a bending of the control line towards the unknown position, as in position 2, indicated the presence of the HM factor and allowed a highly sensitive test for the HM factor's presence.

Relative concentrations of the HM factor were determined by a single-diffusion method described by Hayward and Augustin (1957). In this method the antiserum is incorporated into the agar at 5 percent concentration and serial dilutions of the fluid bearing the HM factor are introduced into wells in the agar. The end point, the highest dilution at which a visible ring can be observed around the well, is referred to as the titer of the solution for the HM factor. Figure 2 illustrates the reactions of serial dilutions of HM factor from an extract from eggs of starry flounder (*Platichtys stellatus*) with the antiserum used in this study. (The preparation of both the extract and the antiserum is described below.) The end point is at the 1/160 dilution.

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[3] The medium in this study had the following composition: Difco agar, 1.5 percent; sodium chloride, 0.72 percent; sodium citrate, 0.6 percent; merthiolate, 0.01 percent; trypan blue, 0.01 percent. The pH was adjusted to 6.7.

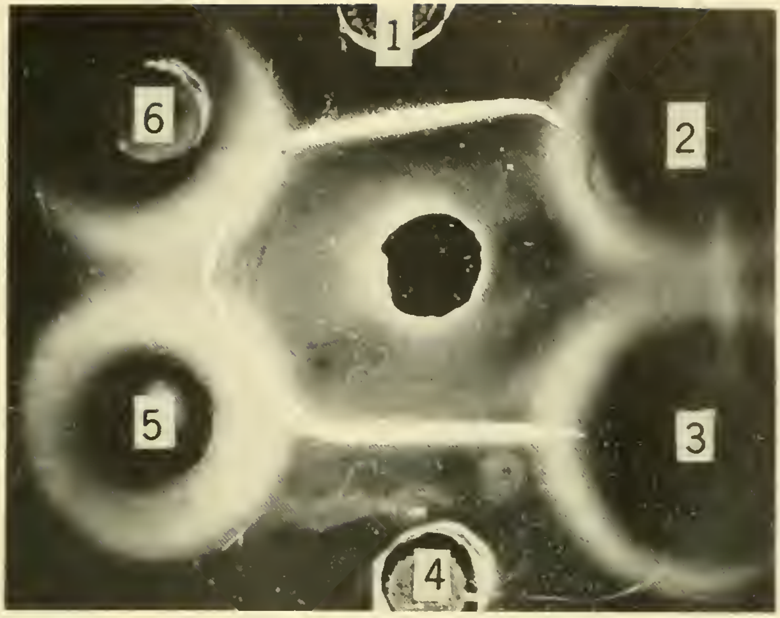

FIGURE 1.—Reactions on typical double-diffusion slide demonstrating tests for presence of HM antigen in kidney-tissue fluids of female English sole. Magnification 5X.

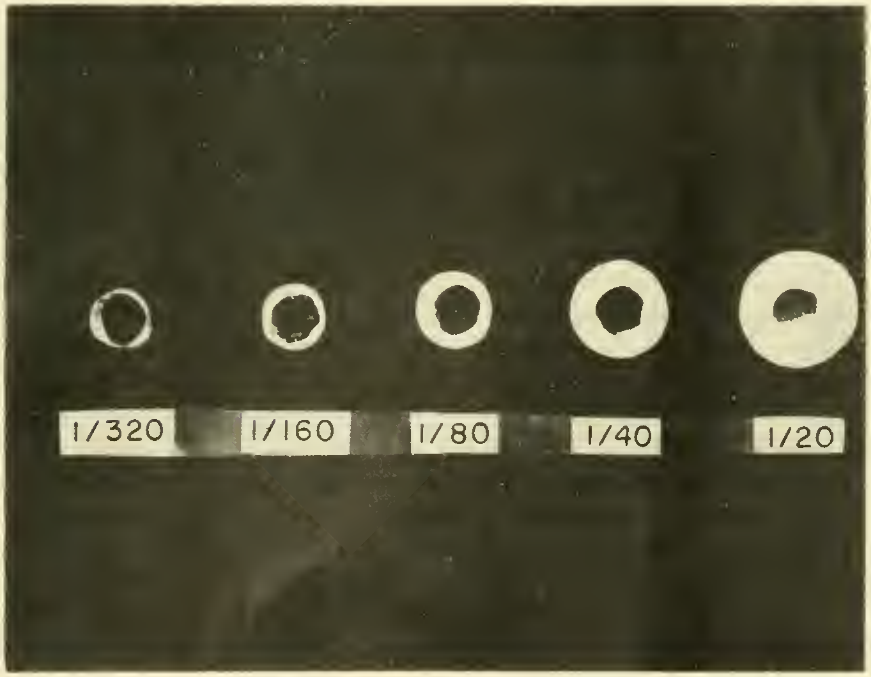

FIGURE 2.—Demonstration of single-diffusion technique to estimate relative concentrations of HM antigen. End point is seen at 1/160 dilution. Magnification 2.5X.

PRODUCTION OF ANTISERUM

The antigenic substance used for production of antisera was a vitellin preparation from starry flounder eggs. This preparation met the classical biochemical criterion for vitellin, since it was the water-insoluble fraction of the egg yolk (Jukes and Kay, 1932). The preparation was made in the following manner: extraction was in a Waring Blendor[4] from 1 part of eggs to 3 parts 1 percent saline solution. One part of the supernatant obtained after centrifugation at 10,000 r.p.m. for 20 minutes was diluted with 11 parts distilled water, and the resulting precipitate was dissolved in 1 percent saline, reprecipitated, and redissolved. The vitellin preparation was utilized in this final form for immunization procedures. Although different injection routes were used and the vitellin preparation was injected both with and without adjuvants, consistently uniform antisera were produced in the five rabbits that were stimulated. Because of this uniformity, a single pooled reagent composed of numerous bleedings from all of the rabbits was made and used throughout this study.

The antibody specificities appeared to be directed toward one or more of the starry flounder's vitellin antigens. The pooled antiserum cross-reacted with serum of mature females of all pleuronectid species tested. Reactions with sera from males were observed only infrequently. These reactions were invariably weak and are discussed in a later section.

COLLECTION OF SAMPLES

Collection dates and numbers of English sole sampled are listed in table 1. All samples were collected by the University of Washington research vessel *Commando* at the Port Orchard area of Puget Sound. Only female English sole were taken. These fish, with the exception of the March sample, were randomly sampled over a variety of lengths. This sample was biased toward smaller individuals with relatively undeveloped ovaries. This bias was based on the relatively high frequency of the HM factor in smaller females in the two previously collected samples; the data for the March sample reflect this bias. Random sampling was resumed through the remainder of the investigation.

Collection of an adequate blood sample from English sole was found impractical, and all qualitative determinations for the HM factor were made from the fluids expressed from kidney tissue. When quantitative data were required, blood samples were collected from larger individuals by cardiac puncture.

The collection data for the halibut samples are presented in table 2. A sufficient blood volume was available from the individual halibut to use serum for determination of the HM factor, although parallel samples of kidney tissue were collected from most fish. All samples were collected under the direction of the International Pacific Halibut Commission.

TABLE 1.—*Collection dates and number of female English sole in samples, Port Orchard area, Wash.*

Collection date	Fish	Collection date	Fish
1962	*Number*	*1963*	*Number*
Dec. 27	30	July 3	25
1963			
Feb. 5	38	July 23	41
Mar. 7	63	October 22	55
June 4	42	November 23	58

TABLE 2.—*Date and areas of collection, number of individual samples, and source of HM antigen for halibut*

Collection date	Area	Fish		Source of HM antigen	
		Female	Male	Serum	Kidney
1960		*Number*	*Number*		
Mar. 25	Queen Charlotte Sound	27	13	x	—
1962					
May 11	Cape Flattery	6	10	x	x
June 6[1]	Queen Charlotte Sound	41	0	x	x
1963					
Feb. 2	Cape Flattery	7	6	x	x
May 23	Cape Flattery	6	15	x	x

[1] Serum collected day of capture; fish eviscerated and iced at this time and kidney fragments collected in port 4 days later.

AGE DETERMINATIONS

Age determinations in both halibut and English sole were made from otoliths. Personnel of the International Pacific Halibut Commission made age determinations of the halibut. English sole otoliths were treated in papain as described by Pruter and Alverson (1962) and read by the senior author.

COMPARISONS OF HM CONCENTRATION IN SERUM AND KIDNEY FLUIDS

The need to use kidney tissue to obtain qualitative data on the HM factor in English sole required us to compare concentrations of the HM factor in kidney-tissue fluids and blood serum of the same individuals.

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[4] Trade names referred to in this publication do not imply endorsement of commercial products.

Table 3 makes such a comparison in 10 females taken a few weeks preceding the spawning season. An end-point fluctuation of plus or minus one serial dilution can be anticipated as part of the experimental error inherent in the technique (Kabat and Mayer, 1961). Only one fish exceeded this range.

TABLE 3.—*Comparative titers of HM factor in kidney-tissue fluid and serum of 10 English sole*

Fish number	Kidney fluid titer*	Serum titer*
1	32	64
2	32	64
3	64	64
4	64	64
5	64	128
6	32	32
7	32	32
8	64	32
9	32	128
10	32	32

*Reciprocal of last positive dilution.

In 19 female halibut, where kidney fluid and serum samples were obtained from freshly caught individuals, identical qualitative results were observed for every fish. In the halibut sample taken during June 1962, kidney fragments were obtained from carcasses that had been eviscerated and iced for 4 days, but serum samples were obtained from the same fish when freshly taken. Qualitative tests were made with both serum and kidney fluids. Quantitative tests were made with those sera which gave positive double-diffusion reactions (table 4). The only disagreements between the qualitative data for the kidney-tissue fluids and serum were the three individuals with the lowest serum concentration. The 4-day icing of the cleaned halibut carcass doubtlessly diluted the HM concentration in the adhering kidney fragments; it seems likely all tests would have agreed if the kidney tissue had been fresh.

TABLE 4.—*Comparison of HM titer of blood serum in halibut with double-diffusion reaction of kidney-fragment fluids collected from the same individuals 3 to 4 days after evisceration and icing*

Fish	Serum titer*	Kidney fluid reaction	
		Positive	Negative
Number		*Number*	*Number*
6	256	6	0
7	128	7	0
4	64	4	0
1	32	1	0
2	16	2	0
1	8	0	1
1	4	0	1
1	2	0	1
18	No reaction	0	18

*Reciprocal of last positive dilution.

The above evidence indicates that serum and freshly taken kidney-tissue fluids can be used interchangeably with considerable confidence for detection of the HM factor in these two species when qualitative data are desired.

ANALYSIS OF DATA ON ENGLISH SOLE

The six stages used by Hagerman (1952) to describe development of the ovary in the Dover sole were modified in the following manner to describe the development in the English sole:

Immature:

A. Ovaries very small (generally less than 1 g.), white, transparent, and somewhat gelatinous.

Mature:

B. Developing. Ovaries enlarging, becoming yellowish and opaque. Developing egg visible macroscopically.

C. Gravid. Ovaries very full of yellowish granular eggs.

D. Spawning. Ovaries full of transluscent eggs which run under slight pressure.

E. Spent. Ovaries flaccid; ovarian membrane vascular and sac-like.

F. Resting. Ovaries firm, white, transluscent, and somewhat gelatinous. Distinguished from stage A by the greater size.

The scale was not universally applied in this study owing to the overlap among the various stages. Stages A and F, in particular, were often difficult to distinguish; however, in November through February, including the peak of spawning in December and January (Holland, 1954; Harry, 1959), the stage A ovaries were distinct because stage F ovaries were lacking. All individuals taken during this period with ovaries in stages B through E were HM positive.

Certain individuals with stage A ovaries surprisingly were HM positive during the spawning season (table 5). Maturity classifications were made on these gonads, which were fixed in formalin. When state of maturity is not listed, the ovaries had been sectioned for histological examination before any external maturity classification was attempted. The two individuals with mature gonads had ovaries in stages B and C, and all gonads classified as immature represented stage A. The HM-positive individuals with stage A gonads from the November samples might have matured later in the spawning season. It is unlikely, however, that the two HM-positive fish with immature gonads from the February sample would have spawned during that season, since all ovaries collected subsequently, through the July sample, were immature or spawned out.

Preliminary results of histological studies being carried out on English sole gonads by Kathleen Ladue, of our staff, were available for the lower two fish from the February sample listed in table 5. Although both were HM positive, only the ovary of the last individual showed atretic follicles as evidence of having spawned; the ovary of the other gave no histological evidence of maturing ova. This evidence supports the previous implications that the HM factor occurs in certain female English sole during the spawning season or seasons preceding that in which they are destined to spawn initially.

Table 5.—*HM-positive female English sole from November, December, and February samples that had gonads weighing less than 1 g., Port Orchard, Wash.*

Month of capture and maturity classification	Gonad weight	Standard body length	Age group
1963	*Gm.*	*Mm.*	
November			
Immature	0.2	207	III
Immature	.5	208	III
Immature	.5	225	III
Mature	.7	249	II
Immature	.7	250	III
Immature	.7	257	III
Immature	.9	265	III
1962			
December			
	.8	254	III
Mature	.9	245	II
1963			
February			
Immature	.5	247	II
Immature	.6	235	II
	.8	268	II
	.8	254	II
	.8	265	III

Table 6 lists the frequency of the HM factor in the various samples by age. The samples are grouped by age to follow the ovaries from the developing stage through the resting stage. Samples taken after the height of the spawning season (December and January) through July are assigned to the age they had during the spawning season, because up to July the ovaries are progressing towards the resting stage. The October and November samples are assigned to the age that they would have had at the next spawning season, because the ovaries are maturing during these months. Thus a fish entering its fourth year of life in January would be included in age-group III if taken in July, and age-group IV if taken in October.

The HM factor occurred initially in age-group II in the fish sampled in this study. The possibility of its presence in group-I fish is not ruled out because insufficient numbers of the group were sampled.

At a given age the highest frequency of the HM factor appears in the December sample at the peak of the spawning season. Frequency generally decreases through July but increases again in October and November. The occurrence of a lower HM frequency in II- and III-group fish for the March sample than for either the June or July samples is very likely the result of the bias described under Methods and Materials regarding the collection of that sample.

Table 6.—*Frequency of the HM factor in the various age groups of female English sole, Port Orchard, Wash.*

Month and item	Age group				
	I	II	III	IV	V[1]
1962					
December:					
Total number of fish		5	14	8	
Number positive		4	12	8	
Percentage positive		80	86	100	
1963					
February:					
Total number of fish	1	34	3		
Number positive	0	10	1		
Percentage positive	0	29	33		
March:					
Total number of fish	9	43	8		
Number positive	0	2	1		
Percentage positive	0	5	13		
June:					
Total number of fish		25	10	3	3
Number positive		8	7	3	3
Percentage positive		32	60	100	100
July:					
Total number of fish		34	16	5	11
Number positive		4	3	1	6
Perentage positive		13	19	20	55
October:					
Total number of fish		12	37	1	5
Number positive		4	26	1	5
Percentage positive		33	60	100	100
November:					
Total number of fish		11	39	5	
Number positive		2	29	3	
Percentage positive		14	74	60	

[1] Age-group V and older.

Figure 3 is a plot of the seasonal fluctuation of the HM factor with body length. Fish 22 to 25 cm. long were combined in the December sample because the separate groups had few individuals.

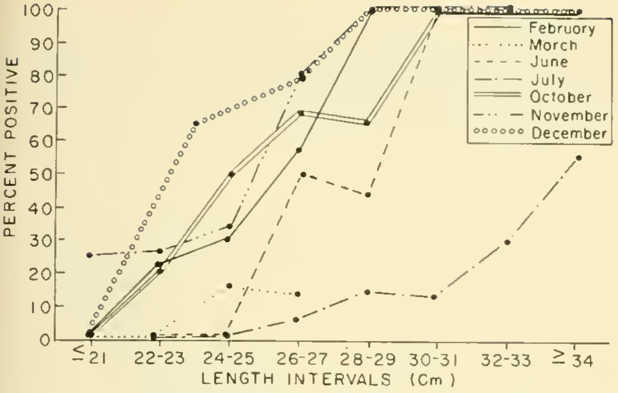

FIGURE 3.—The relation of the frequency of the HM factor to length in female English sole in different months, 1962–63, Port Orchard, Wash.

A distinct seasonal change took place between the spawning in December and the resting stage in July; during this period the HM frequency for a given length interval generally decreased. In the October and November samples, as the ovaries developed for the next spawning season, the HM frequencies in the various length intervals again increased.

Figure 3 does not take into account any growth between the December sample and subsequent collections. If seasonal growth increments were considered, most individuals 26 to 29 cm. long in December would be 30 to 33 cm. long in July. This statement is based on the assumption that El Sayed's (1959) growth estimates for English sole from Holmes Harbor in Northern Puget Sound are applicable to the Port Orchard population. A comparison of the HM frequency in these two length intervals in December with the next higher interval in July still indicates a striking variation of frequency.

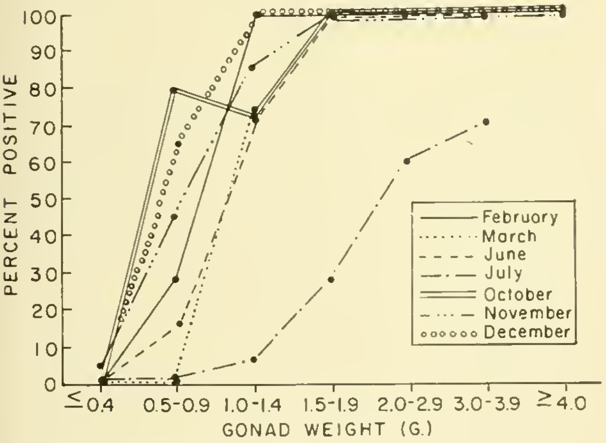

FIGURE 4.—The relation of HM frequency to gonad weights in female English sole, 1962–63, Port Orchard, Wash.

Ovarian weight and HM frequency are related (fig. 4). Gonad weight and HM frequency increased simultaneously. A qualitative seasonal variation in the factor's presence is again indicated. All ovaries weighing more than 1 g. that were taken during or immediately following the spawning season were from HM-positive individuals. Even a considerable number of the largest ovaries taken during the resting stage were from HM-negative individuals; HM frequency decreased as the ovarian mass decreased.

The relation between gono-somatic ratio (gonad weight expressed as percentage body weight) and HM frequency is generaly similar to that between gonad weight alone and HM frequency (fig. 5).

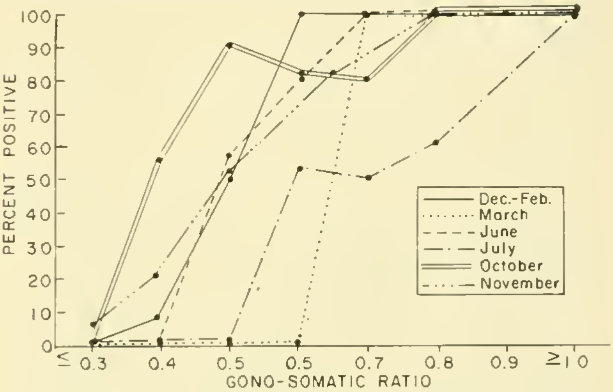

FIGURE 5.—The relation of HM frequency to gono-somatic ratios in female English sole.

The gonad weight shows the relation more clearly than the gono-somatic ratio, however, suggesting that the qualitative seasonal variations of the HM frequency are dependent more on the absolute weight of the gonad than on its mass relative to body weight.

ANALYSIS OF DATA ON HALIBUT

The HM frequency of the various halibut samples is given according to length in table 7. Fish of various ages were combined in the length intervals because of the small samples. The criterion for maturity of halibut ovaries was the presence of macroscopic ova. Personnel of the International Pacific Halibut Commission made all maturity estimates. The HM factor was detected in the serum from all female halibut that were estimated to be mature.

In the sample of June 5, 1962, which gave the best representation of different ages within a given length interval, no indication of an age dependency was detectable. In spite of the small sample sizes, the frequency of the HM factor seems to increase in length in all samples but that of February 23, 1963. This exceptional situation is discussed below.

Table 7.—*HM frequencies in female halibut according to length*

Date of collection	Length (cm.)							
	<85		85-100		101-110		>110	
	HM +	HM −	HM +	HM —	HM +	HM —	HM +	HM —
	Number of fish	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*
1963 Feb. 23	2	0	3	1	1	0	0	0
1960 Apr. 20	0	1	1	3	0	1	7	0
1963 Apr. 23	0	0	0	2	1	1	1	1
1962 May 11	0	0	0	2	2	0	2	0
June 5	0	0	6	10	8	8	9	0

Note.—Sampling areas shown in table 2.

As pointed out previously, we detected the HM factor during the spawning season in the serum of certain individual English sole with immature ovaries; apparently a similar condition exists in halibut. Two 76-cm. females taken in the February 23, 1963, sample at the peak of the spawning season were HM positive. [Thompson (1915) defined the spawning season for halibut as extending from December to April with the peak in February.] These fish were smaller than the minimum length reported by Thompson for mature females captured from areas included in this study, and the small ovaries did not give external indications of development. The records of serum titers of the HM-positive females in the sample of February 23, 1963, show that the two HM-positive females which were judged immature had very low titers whereas the mature individuals had titers exceeding a serum dilution of 1/250 (table 8). These findings suggest that a quantitative means may be used to distinguish maturing and mature females from immature females in which the HM factor may also be present.

In the discussion of table 4 in a preceding section, serum titers were compared with qualitative reactions of kidney-tissue fluids from the halibut sample taken on June 6, 1962. The only failures of parallel reactions were in individuals having serum dilution titers of one-eighth or less. This information indicates that kidney-fragment fluids may be useful in researchers' obtaining data relative to maturity and sex by sampling the eviscerated fish in the commercial catch upon arrival in port.

Table 8.—*Serum titers and maturity estimates of HM-positive females from halibut sample of February 23, 1963, taken at Cape Flattery, Wash.*

Number of fish	HM serum titer[1]	Estimate of maturity[1]
1	<2	Immature
7	<2	do
2	512	Mature
6	512	do
8	256	do
11	1,024	do

[1] Reciprocal of last positive dilution.

PRODUCTION OF HM FACTOR BY MALES

The link connecting estrogen with the production of serum components related to maturity has been determined by a number of investigators of birds, through the production of these components in males and immature females after artificial stimulation with estrogenic hormones (McDonald and Riddle, 1945; Urist and Schjeide, 1961). Bailey (1957), Urist and Schjeide (1961), and Ho and Vanstone (1961) have likewise demonstrated that artificial stimulation with estrogenic hormones produces a blood serum situation similar to that of the mature female in the teleosts *Carassius auratus*, *Paralabrax clathratus*, and *Oncorhynchus nerka*, respectively. We attempted this procedure in this study with four English sole maintained in an aquarium at the University of Washington College of Fisheries. Each fish was injected intramuscularly with 1 ml. of an aqueous suspension of estrone (5 mg./cc.). Two fish survived the initial handling (table 9). Data for the fish firmly establish the presence of the HM factor as a consequence of introducing the estrogenic hormone. Although a control bleeding was not made for fish No. 1, the rise in titer between the first and second bleeding establishes beyond doubt the effect of the estrone injection.

The HM factor was in low concentration in two male halibut taken during the spawning season. The possibility of contamination cannot be excluded because both were taken immediately following the collection of a sample from an HM-positive female, although precautions were taken to minimize contamination.

TABLE 9.—*Effect of estrone injections on the occurrence of the HM factor in the serum of male English sole*

Fish number and time of bleeding	HM reaction	Titer[1]
No. 1:		
Prior to injection	—[2]	—[2]
48 hours after injection	+	8
144 hours after injection	+	256
No. 2:		
Prior to injection	0	0
48 hours after injection	+	<8
144 hours after injection	+	256

[1] Reciprocal dilution. [2] No control bleeding.

The production of the HM factor in the serum of male English sole after estrogenic stimulations and the natural occurrence of the factor in male halibut during the spawning season indicate that males should be included in investigations of the HM factor. The natural occurrence of the factor in males may have a number of causes. Although the testes of the HM-positive male halibut appeared normal, the presence of the factor may have been due to low-level secretions of estrogenic hormones. Hermaphoditism has been reported in a diverse range of teleosts, including clupeids (Fowler, 1912), salmonids (Ross, Yasutake, and White, 1963), siluroids (Singh and Sathyaneson, 1961), cyprinodonts (Chidester, 1917), centrachids (James, 1946), and scombroids (Uchida, 1961). A further possibility is the stimulation by estrogenic hormones of exogenous origin through ingestion of mature females of smaller species of flatfish or possibly fish from other families. Estrogenic hormones are effective when administrated orally to mammals and presumably could be similarly effective in fish.

BIOLOGICAL IMPLICATIONS OF THE PRESENCE OF THE HM FACTOR

The English sole has been demonstrated to have a qualitative seasonal variation of the HM factor. The factor occurs first during the spawning season, at least as early as the second year in some individuals. After the spawning season through at least midsummer, fewer and fewer individuals retain the factor in the serum. As a new spawning season approaches, the factor gradually reappears.

Both the disappearance and the reappearance of the factor are more pronounced with increase of body length and ovarian mass. This relation may be the result of resorption of residual vitellin retained with the ovary, since the large ovaries retain a greater volume of unspawned ova.

A qualitative seasonal variation was not found in mature halibut, but we lack samples taken later than June. Thompson (1915) reported a continuous development of the ova which are to mature in the succeeding generation in the spent halibut ovary; vitellin synthesis may be a perennial process in the mature female halibut. The detection of serum vitellin in postspawning Atlantic salmon (*Salmo salar*) by Fine and Drilhon (1964) suggests its perennial occurrence in this species.

The presence of the HM factor during spawning season in immature females of both species indicates that such an occurrence may be widespread among the Pleuronectidae. Incomplete maturation preceding initial spawning in the Pleuronectidae has been reported previously. Thompson (1915) stated that contemporary investigators had found some ova in immature pleuronectid females which appeared ready to ripen but which failed to do so because the ovary, as a whole, was not yet ready. Franz (1910) reported finding this condition most marked in plaice during the last winter preceding initial spawning.

PRACTICAL APPLICATIONS OF THE HM FACTOR

As a practical procedure, the determination of the HM factor appears to have its greatest potential value in the larger pleuronectid species. In large species such as halibut or starry flounder, the sex cannot be determined at sight, except in ripe individuals. Small samples of blood taken at the time of tagging could yield information on sex and maturity without endangering the fish. Repeated bleedings of four starry flounders kept in captivity did not appear to endanger these fish. Routine practical applications to smaller species seem less likely. The sexes of smaller flatfish species, such as English sole, are generally evident by external examination; and bleeding English sole, where required in this study, caused high mortality. Evisceration of the commercial halibut catch at sea does not preclude practical application, since analysis of kidney-fragment fluids can be made after the catch arrives in port. On the other hand, smaller species are brought to port in the round and sex information can be obtained directly. Smaller species, however, are frequently more readily available in greater numbers; they are valuable for clarification of general principles which may be applied to other species as well.

SEPARATION OF MATURE FEMALES FROM OTHER HM-POSITIVE INDIVIDUALS

Separation of HM-positive males and immature females from mature females appears possible by quantitative means. The HM serum levels of mature female halibut taken during the spawning season had titers above 200, whereas the titers of HM-positive males and immature females, which were found only at this time, were less than 2.

An extension of the single diffusion quantitation, as used in this study, may be applied where routine quantitation is required. From figure 2 it can be observed that the diameter of the precipitin ring decreases regularly as the HM concentration decreases. A measurement of the diameter of the precipitin ring formed by the undiluted fish serum could give the approximate titer.

AREAS FOR FURTHER INVESTIGATION

Several areas for further study are evident. More frequent and larger samples are desirable. As indicated above, routine quantitation may be necessary during the spawning season, and a knowledge of the quantitative seasonal fluctuation of the HM factor in a given species would be useful. Perhaps the relative HM concentration can be related to such factors as age, weight, or fecundity. More extensive histological examinations of the ovary would help, and a similar examination of the pituitary gland may establish more fundamental criteria for the occurrence of the factor. A biochemical assay might indicate that the composition of the factor in fishes is related to analogous components in other vertebrates.

THE BROADENING APPLICATION OF SEROLOGY IN FISHERY RESEARCH

Serological techniques have had increasing application in fishery problems during recent years. This research has been directed mainly toward racial studies of serum antigens or red blood cell antigens. Many of the current approaches to serological investigations of populations were discussed in a symposium moderated by Cushing (1962), and the subject has been reviewed recently by Marr and Sprague (1963) and Cushing (1964).

Antigenic differences at species level have also been investigated. Ridgway and Klontz (unpublished data) and Sindermann (1962) have found distinct species-specific antigenic characteristics in red blood cells and serum of species of Pacific salmon and Atlantic clupeiods, respectively. Ridgway (1963) reported species-specific antigens in muscle tissue of certain tuna species, in addition to species-specific blood serum components. This finding offers a possible serological means of distinguishing larvae of these species.

We hope that this study will help broaden the interest in application of serological methods to other areas of fishery biology. Because components similar to the HM factor have been detected in a diverse range of teleosts, a similar approach presumably could be used throughout this class of vertebrates. We feel that this approach can be a valuable supplement to investigating maturity in fish, though perhaps not universally applicable.

SUMMARY

A serological investigation of a serum vitellin factor in mature and maturing female flatfish was made on English sole and Pacific halibut. Immunodiffusion techniques with antisera prepared in rabbits stimulated with egg vitellin extracted from starry flounder eggs were used to detect the factor. In English sole the factor's occurrence was compared with age, length, gonad weight, and gono-somatic ratio. A qualitative seasonal variation was found; individuals with heavier ovaries during the summer were more likely to retain the factor in the serum. The presence of the factor in female halibut was compared with length, age, and maturity. A qualitative seasonal variation in mature halibut could not be studied because no samples were available during the summer or autumn. The factor was found in some immature females of both species during their spawning seasons. Production of the factor in male English sole by injections of estrogenic hormones associates synthesis of the factor in females with production of estrogen. Determination of the factor appears to have potential value as a supplement to other means of investigating maturity, particularly in large species.

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EFFECT OF WATER VELOCITY ON PASSAGE OF SALMONIDS IN A TRANSPORTATION CHANNEL

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ABSTRACT

Passage times of fish at velocities of 1 and 2 feet per second were compared in a 4-foot wide transportation channel, with a water depth of 6 feet. The timing zone was about 100 feet long.

Passage times did not differ significantly between water velocities for any one of three species: chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), and sockeye salmon (*Oncorhynchus nerka*). The two salmon species moved faster than steelhead trout at both water velocities.

Transportation channels for migrating adult fish are part of the fish-passage facilities at many dams. These channels vary somewhat physically, but all have the primary purpose of providing a passage area leading either to or from the fish ladders or other passage facilities. Most of the large dams on the Columbia River—Bonneville, McNary, and The Dalles, for example—have a multiple-entrance collection channel on the downstream side of the powerhouse which also serves as a transportation channel. In addition, independent channels are occasionally provided at some dams to pass fish from a single major entrance to a distant fishway. The Dalles Dam is equipped with both types (U.S. Army Corps of Engineers, 1957). These channels make it possible for one fishway to serve two or more collection points. Some channels are nearly a quarter mile long and may require up to 1,000 cubic feet per second (c.f.s.) of water for operation.

Water velocity in a transportation channel is important from the standpoint of fish passage as well as water use. Clay (1961) reported that the accepted standard velocity for ensuring continuous migration of fish through open channels is near 2 feet per second (f.p.s.). Preliminary experiments at the Fisheries-Engineering Research Laboratory at Bonneville Dam indicated that a velocity considerably less than 2 f.p.s. might be satisfactory for passage of salmonids. If so, velocity standards for transportation channels could be lowered and less water used without impeding the passage of migrating fish.

The purpose of this study[1] was to determine if salmonids would move up a transportation channel as rapidly in a water velocity of 1 f.p.s. as in 2 f.p.s.

EXPERIMENTAL EQUIPMENT

The study was made in the Fisheries-Engineering Research Laboratory at Bonneville Dam on the Columbia River. Details of the laboratory were described by Collins and Elling (1960). The experimental transportation channel (fig. 1) was 4 feet wide, 91 feet long, and operated at a water depth of 6 feet. Fish were timed over a distance of about 100 feet. (This included a short introductory area extending from a release compartment to the channel.) Water velocity was controlled by regulating the head on a weir located between the flow-introduction pool and the test channel. Headwater elevations producing velocities of 1 and 2 f.p.s. were determined before the experiment was started.

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[1] Research financed by the U.S. Army Corps of Engineers as part of a broad program to provide design criteria for more economical and efficient fish-passage facilities at Corps projects on the Columbia River.

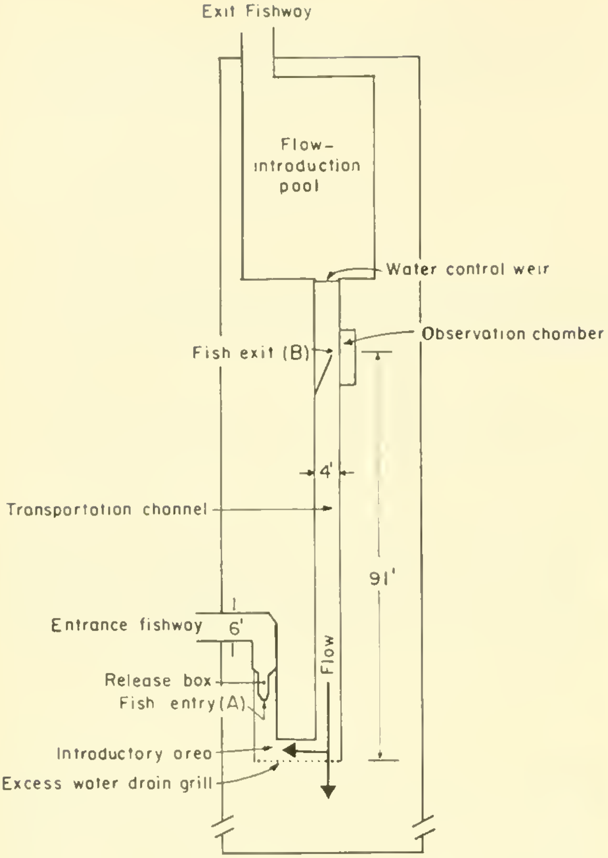
Exit Fishway
Flow-introduction pool
Water control weir
Observation chamber
Fish exit (B)
4'
Transportation channel
91'
Entrance fishway
6'
Release box
Fish entry (A)
Flow
Introductory area
Excess water drain grill

FIGURE 1.—Diagrammatic plan view of laboratory showing transportation channel and timing zone (A to B).

Velocities were measured with a cup-type current meter.

The channel was lighted by 1,000-watt mercury-vapor lights placed 6 feet apart and suspended 6 feet above the water. Light readings at the surface averaged about 700 foot-candles, which approximates light intensity on a bright cloudy day.

PROCEDURE

Salmonids used in these tests were diverted from the Washington shore fishway at Bonneville Dam. They ascended a short entrance fishway to the laboratory. Varying numbers of fish were used in each test, depending on seasonal abundance of the different species. Each fish entering the laboratory was tested only once. After a fish had completed passage through the test facility, it left the laboratory through a small exit fishway and entered the main fishway about 200 feet upstream from the laboratory.

Fish of all sizes were used; however, on a few occasions, fish were rejected because of severe cuts or other obvious physical injuries. No distinction was made as to sex.

EXPERIMENTAL DESIGN

A 2 by 2 Latin Square design used in these tests allowed 4 days (2 days at each velocity) for each test. The experiment consisted of four separate tests—two with chinook salmon (*Oncorhynchus tshawytscha*) and one each with steelhead trout (*Salmo gairdneri*) and sockeye salmon (*Oncorhynchus nerka*).

TIMING FISH

Fish entered a release compartment (fig. 2) where they were identified as to species and released individually into the test area. Only one fish was permitted in the channel at any one time.

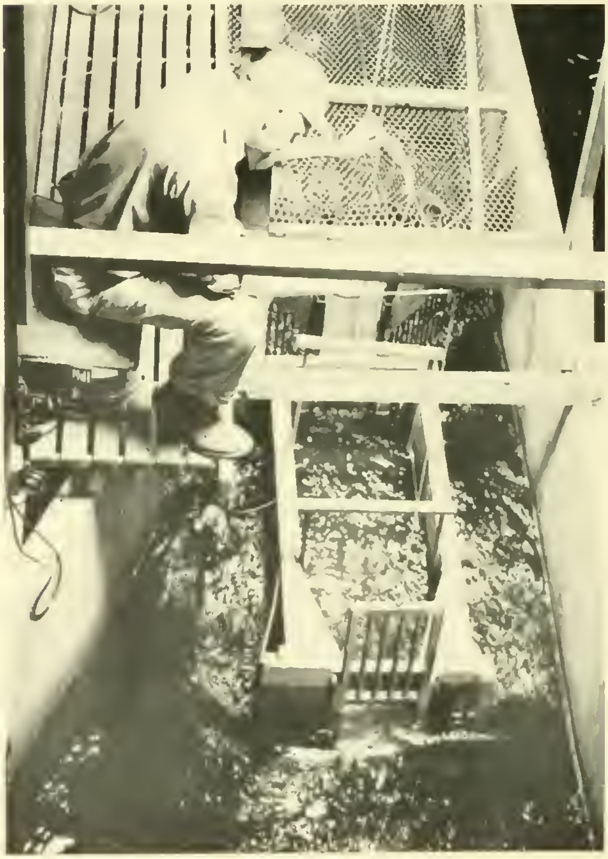

FIGURE 2.—Release compartment. Operator has raised gate (foreground) to allow fish to enter test area.

The timing zone (A to B, fig. 1) extended from the release compartment (A) to the exit area (B) at the upper end of the channel. A deflecting grillwork (fig. 3) directed fish toward an observation window at the point of exit. This arrangement ensured accurate observation and timing of the fish when visibility was limited owing to turbid water. The time of entry and exit for each fish was registered on a special time-event recorder. If a fish had not completed passage of the channel within 45 minutes after time of entry, it was removed and another fish was introduced.

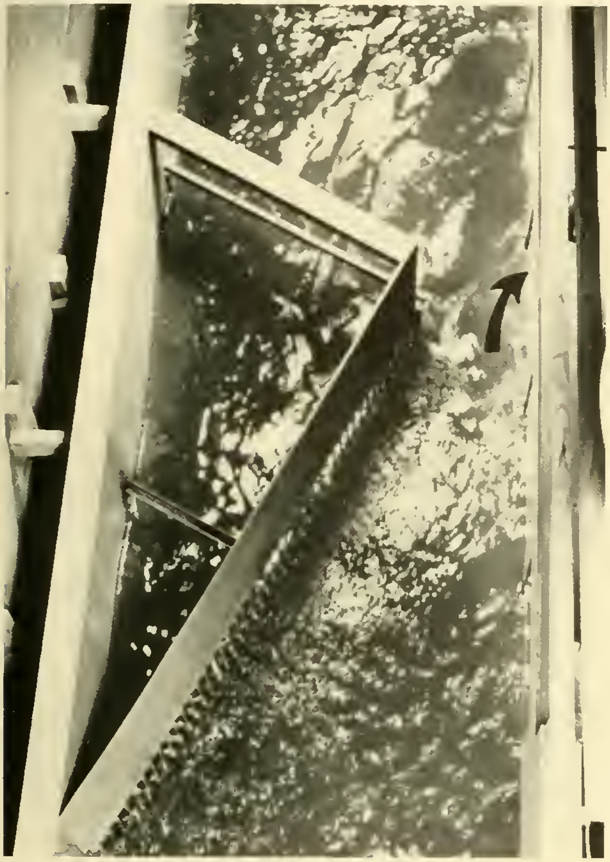

Figure 3.—Exit area of test channel viewed from above. Grill on left foreground deflects fish toward viewing area (arrow) of submerged observation chamber. Flow is toward foreground.

ANALYSIS OF PASSAGE TIME

The effect of water velocity on fish passage was determined by measuring the time required for the fish to pass through the channel. Ninety-five percent confidence intervals about the median (Dixon and Massey, 1957) were applied to test for significance of differences between passage times at the two velocities. As used here, the median is the passage time of the median fish of all fish tested in each group, including those fish that failed to complete passage within the arbitrary 45-minute time limit. Computations of the mean passage time include only those fish that completed passage of the test channel within 45 minutes.

PASSAGE TIME IN RELATION TO WATER VELOCITY

Comparisons of time required to pass through the test channel at the two velocities are given by species in the following subsections.

CHINOOK SALMON

Tests with chinook salmon were made during two periods—May 8–11 and June 12–15, 1962. Fish in the early period are normally called spring-run and those in the latter period, summer-run chinook salmon. Median passage times in the May test at water velocities of 1 and 2 f.p.s. were 3.4 and 3.9 minutes, respectively (table 1). Results of the June test were similar. Median passage times in the two velocities did not differ significantly between velocities or between tests. Mean passage times, given for comparison, suggest similar trends. In both tests, however, chinook salmon took slightly more time to pass through the channel at 2 f.p.s. than at 1 f.p.s. (fig. 4). This difference corresponds with observations by Weaver (1963), who found that chinook salmon moved more slowly as velocity increased in the range of 2 to 8 f.p.s.

Table 1.—*Median and mean passage times of chinook salmon in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., May and June 1962*

Test period	Water velocity	Fish tested	Passage time			
			Median	Lower limit[1]	Upper limit[1]	Mean
	F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
May 8–11	1	37	3.4	2.7	5.5	4.7
	2	44	3.9	3.2	4.5	[2]4.9
June 12–15	1	45	3.1	2.5	4.4	4.8
	2	75	3.6	2.7	4.2	5.3

[1] 95-percent confidence intervals about the median

[2] One fish failed to complete passage within the 45-minute time limit and was not included in computation of the mean.

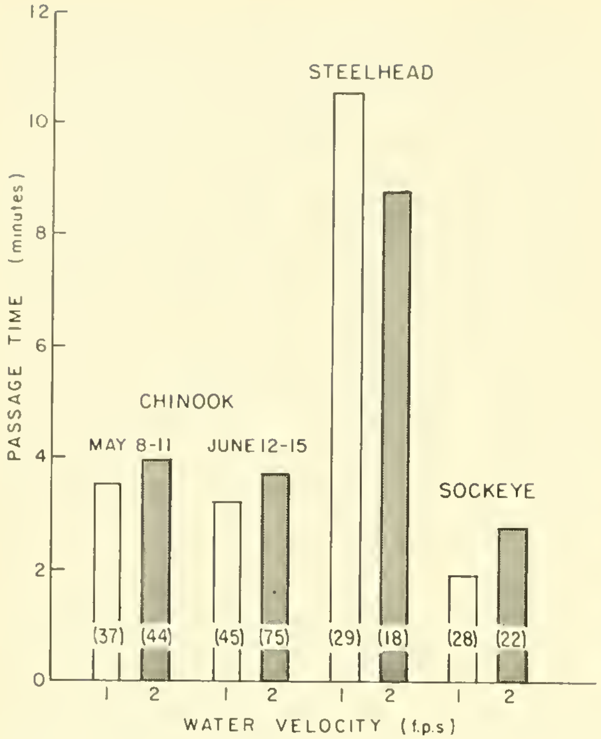

Figure 4.—Median passage times of chinook salmon, steelhead trout, and sockeye salmon in a transportation channel at water velocities of 1 and 2 f.p.s., 1962. Numbers of fish tested are shown in parentheses near the base of each bar.

STEELHEAD TROUT

Median passage times of steelhead trout at water velocities of 1 and 2 f.p.s. were 10.6 and 8.8 minutes, respectively (table 2). This difference was not statistically significant. Mean passage times were similar to the medians. Steelhead trout moved somewhat faster at the higher velocity, in contrast to the difference in chinook salmon (fig. 4). Weaver (1963) observed similar performances among steelhead trout, i.e., faster movement as water velocity increased.

In comparison with the other species tested, steelhead trout obviously spent considerable time in the test channel. Given suitable hydraulic conditions, steelhead trout frequently remain in favored pools or runs for varying periods of time before proceeding upstream. This characteristic possibly accounts for the relatively slow passage times of this species in the present tests.

SOCKEYE SALMON

Performances of sockeye salmon at the two water velocities were similar to those of chinook salmon. Both the median and mean passage times (table 3) give evidence of a slightly faster passage at the lower velocity. The difference between median passage times, however, was not significant.

Table 2.—*Median and mean passage times of steelhead trout in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., July 30–August 2, 1962*

Water velocity	Fish tested	Passage time			
		Median	Lower limit[1]	Upper limit[1]	Mean
F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
1	29	10.6	5.4	15.0	[2]9.6
2	19	8.8	3.0	11.0	[3]8.1

[1] 95-percent confidence intervals about the median.

[2] Four fish failed to complete passage within the 45-minute time limit and were not included in computation of the mean

[3] Excludes one fish that did not complete passage within 45 minutes.

Table 3.—*Median and mean passage times of sockeye salmon in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., July 10–13, 1962*

Water velocity	Fish tested	Passage time			
		Median	Lower limit[1]	Upper limit[1]	Mean
F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
1	28	1.9	1.5	3.3	3.1
2	22	2.7	2.0	5.7	[2]4.1

[1] 95-percent confidence intervals about the median.

[2] One fish failed to complete passage within the 45-minute time limit and was not included in computation of the mean.

CONCLUSION

A water velocity of 1 f.p.s. is as suitable as one of 2 f.p.s. for the passage of chinook salmon, steelhead trout, and sockeye salmon in a transportation channel.

ACKNOWLEDGMENTS

Gerald B. Collins and Carl H. Elling assisted in planning the experiments. William S. Davis suggested the experimental design, and the staff at the Fisheries-Engineering Research Laboratory aided in carrying out the work.

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COMPARATIVE ANATOMY AND SYSTEMATICS OF THE TUNAS, GENUS *THUNNUS*[1]

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ABSTRACT

The taxonomic status of the tunas of the world, often placed in the genera *Thunnus, Germo, Neothunnus, Parathunnus,* and *Kishinoella,* is assessed through the use of external morphological and internal anatomical characters. Seven species, all included in the single genus *Thunnus,* are considered valid: *T. thynnus,* the bluefin tuna; *T. alalunga,* the albacore; *T. obesus,* the bigeye tuna; and *T. albacares,* the yellowfin tuna, are circumglobal in distribution; *T. atlanticus,* the blackfin tuna, and *T. tonggol,* the longtail tuna, are restricted to the western Atlantic and the Indo-West Pacific, respectively; *T. maccoyii,* the southern bluefin tuna, is known in the southern Pacific and Indian oceans and off northwestern Australia. Two subspecies of *T. thynnus* are recognized: *T. t. thynnus* in the Atlantic and *T. t. orientalis* in the Pacific.

In Part 1 the comparative anatomy is described and characters are given for differentiating the species by means of counts and measurements and by comparison of the skeletal, visceral, and vascular systems. In Part 2 the genus *Thunnus* is characterized with respect to other genera of Scombridae, and for each species a synonymy, a résumé of distinctive characters, discussion of type specimens and nomenclatural problems, and a review of known geographic distribution are given.

The purpose of this paper is to demonstrate that there are, at most, seven species of tunas in the world, and that they should be placed in the single genus *Thunnus* which is circumglobal in distribution and constitutes one of the most important groups of commercial fishes. Much time and money have been expended in gathering meristic, morphometric, anatomical, distributional, and life-history data, yet the systematic and nomenclatural status of the group remains unsatisfactory. Over the years, 10 generic names and 37 specific names have been applied to the seven species which we recognize. The confusion is due, at least in part, to the pelagic habits of all of the species and to their large adult size, which makes specimens difficult to preserve and store and requires that observations be made at the time of collection, often under adverse conditions. Study material over the great size range is not easily obtained, so that growth changes are hard to evaluate. The economic importance of the group has led many biologists to dabble in tuna taxonomy, using variable characters and different means of counting and measuring. Provincialism has caused otherwise competent workers to believe that the kinds of tunas in their home areas are unique and to cling tenaciously to locally established names despite contrary evidence.

Our studies have been built upon the work of a number of previous investigators. We have come to realize, as many of these workers have, the great value of internal anatomical characters as a means of distinguishing tuna species. In this field, Kishinouye (1915, 1917, 1923) pioneered. The most extensive

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and painstaking anatomical descriptions are found in his works and those of Godsil and Byers (1944) and Godsil and Holmberg (1950).

This paper is divided into two major sections. The first part describes and compares the osteology, viscera, vascular system, meristic characters, morphometry, and coloration among the species. The second part considers the systematic position of the genus *Thunnus*. Each species is treated separately, including a synonymy, diagnosis (based on characters from the first section), discussion of nominal species, and outline of geographical distribution.

MATERIALS AND ACKNOWLEDGMENTS

We have examined, measured, and made counts on numerous specimens of all Western Atlantic species. Many specimens taken in pound nets in Cape Cod Bay were made available through the courtesy of John E. Vetorino, Mike Goulart, and Adam Rupkus. Most material for dissection and a large share of the total specimens examined were collected on exploratory longline cruises, by the Bureau of Commercial Fisheries vessels *Delaware* in the Gulf Stream and adjacent waters east to the Azores and *Oregon* in the Gulf of Mexico and Caribbean Sea. For saving valuable specimens and for allowing us to participate in many cruises, we are particularly indebted to Harvey R. Bullis, Peter C. Wilson, and James L. Squire. The late Al Pflueger of Miami, Fla., and Frank J. Mather III of Woods Hole Oceanographic Institution (WHOI), gave us a number of specimens. Edward C. Raney lent us skeletons from Cornell University. Margaret E. Watson of WHOI and Donald P. de Sylva of the University of Miami Institute of Marine Science allowed us to examine other specimens.

Southeast Pacific specimens of *T. obesus* and *T. albacares* were dissected during our participation in cruise 14 of the *Anton Bruun*, part of the South East Pacific Biological Oceanographic Program sponsored by the National Science Foundation. Australian and Japanese tunas were examined in the fish markets of Tokyo and Yaizu. We obtained whole specimens or skeletal material of Pacific species from the Inter-American Tropical Tuna Commission (M. B. Schaefer and Craig Orange); California State Fisheries Laboratory (Phil Roedel and Harold B. Clemens); Bureau of Commercial Fisheries Biological Laboratory, Honolulu (John C. Marr); Nankai Regional Fisheries Laboratory, Kochi, Japan (Hiroshi Nakamura and Shoji Ueyanagi); Tokyo University (Tokiharu Abe); Kyoto University, Maizuru, Japan (Izumi Nakamura and Tamotsu Iwai); Institut Français d'Océanie, Noumea, New Caledonia (Michel Legand); and C.S.I.R.O. Marine Laboratory, Cronulla, Australia (J. C. Moore and J. P. Robins).

Specimens from the Indian Ocean were received from the Nankai Laboratory and from cruises of the *Anton Bruun* made during the U.S. Program in Biology of the International Indian Ocean Expedition. Frank H. Talbot and Michael Penrith provided South African specimens and skeletons.

We examined specimens and skeletons of both Atlantic and Pacific forms at the California Academy of Sciences (W. I. Follett); Stanford University (George S. Myers and Warren C. Freihofer); University of California at Los Angeles (Wayne J. Baldwin); Scripps Institution of Oceanography (Richard H. Rosenblatt); and the U.S. National Museum and skeletons of Pacific and Indian Ocean specimens at Kyoto University, Maizuru (Tamotsu Iwai and Izumi Nakamura) and the Nankai laboratory (Shoji Ueyanagi).

All available types were examined at the Muséum National d'Histoire Naturelle (MNHN), Paris (M. L. Bauchot and C. Roux); at the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden (M. Boeseman); and at the Academy of Natural Sciences, Philadelphia (ANSP) (James E. Böhlke). We received information on types in the Australian Museum in Sydney and the Dominion Museum in Wellington from Frank H. Talbot and J. Moreland, respectively.

We made thorough examinations of viscera and blood vessels on the following (sizes in mm.):

Thunnus alalunga 9 Atlantic (780–1,250), 1 Pacific (992), 2 Indian (ca. 900–970)
Thunnus albacares 15 Atlantic (600–1,515), 4 Pacific (670–911), 11 Indian (601–895)
Thunnus atlanticus 21 (322–665)
Thunnus obesus 17 Atlantic (697–1,545), 5 Pacific (851–1,614), 2 Indian (630–680)
Thunnus maccoyii 3 (712–1,442)
Thunnus thynnus thynnus 10 (316–2,315)
Thunnus thynnus orientalis 3 (614–1,450)
Thunnus tonggol 4 (373–924)

The following complete skeletons (most of which are now in the U.S. National Museum) provide the basis for our analysis. These include a large share of the material of Godsil and Byers (1944) and Godsil and Holmberg (1950). Range of skull lengths, in mm., in parentheses.

- *Thunnus alalunga* 19 Atlantic (125–167), 26 Pacific (99–152), 2 Indian (146–157)
- *Thunnus albacares* 21 Atlantic (98–196), 26 Pacific (49–149), 12 Indian (101–127)
- *Thunnus atlanticus* 26 (51–111)
- *Thunnus obesus* 21 Atlantic (119–215), 5 Pacific (97–237), 4 Indian (112–178)
- *Thunnus maccoyii* 9 Australia (111–219), 4 South Africa (128–218), 4 SE. Pacific (207–238)
- *Thunnus thynnus thynnus* 21 Atlantic (76–335), 1 South Africa (322)
- *Thunnus thynnus orientalis* 40 (34–294), 1 SE. Pacific (290)
- *Thunnus tonggol* 2 East Australia (122–128), 6 Indian (56–99).

Details were corroborated by numerous partial dissections of all species. We also examined many additional skulls, postcranial skeletons, and radiographs.

We are grateful to Daniel M. Cohen, J. A. F. Garrick, Brian J. Rothschild, Donald W. Strasburg, Frank H. Talbot, and Stanley H. Weitzman for making comments on various drafts of the manuscript. Mildred H. Carrington and Gale G. Pasley made most of the figures from our sketches. Alice Holland typed many drafts of the manuscript. John E. Fitch made it possible to use the plate blocks from Godsil and Byers (1944) for figures 20 and 21.

METHODS

Dissections.—Although numerous partial dissections of both preserved and fresh specimens were made, the most thorough work was done with fresh specimens on shipboard or, more often, with frozen specimens in the laboratory. After the fish thawed, colored latex was injected into the arteries and veins through the lateral cutaneous branches that had been exposed by removing the thick skin behind the pectoral fin base. Often the injection mass did not reach the posterior ends of the cutaneous vessels or the posterior commissure, but these vessels ordinarily could be followed rather easily. In the other direction, the injection mass seldom penetrated beyond the liver, partly because the deeper regions were not completely thawed. After the latex had set, the lateral cutaneous system was studied. The ventral wall of the body cavity was then removed and the viscera drawn in situ. The ventral organs were then turned aside or removed to expose the swim-bladder, and this, in turn, was removed and the dorsal fibrous connective tissue cut to expose the kidney and ureters. The most difficult aspect of the dissection involved exposing and tracing the anterior arteries, which lie so far forward and are so deep that they are difficult to reach without mutilating the branchial region. After the appropriate observations were completed, the specimen was fleshed and the skeleton cleaned.

Counts and measurements.—Most external counts and measurements were made on fresh or frozen specimens, some on preserved material, according to the methods described by Marr and Schaefer (1949), with the following exceptions. Our fork length is what they called "total length." We measured length of bony orbit rather than diameter of iris; in our comparisons, therefore, we used only our own data for this character. (We do not recommend this procedure for future workers.) We did not measure "pectoral insertion to insertion first dorsal," or "length longest dorsal finlet," but we made the following measurements not mentioned by Marr and Schaefer: Snout to insertion of pectoral fin, maximum width of body, pelvic fin length, insertion of pelvic fin to vent, tip of depressed pelvic fin to vent (all of which are self-explanatory), snout length (snout tip to front edge of bony orbit), and interorbital width (least distance between dorsal rims of bony orbits formed by frontal bones).

Measurements made by the same worker of the same specimen before and after freezing may differ enough to negate a morphometric difference between species, therefore, all morphometric characters should be used only with rather wide margins for error.

Skeletons.—Skull length was measured from the anterior tip of the vomer to the lower posterior end of the ankylosed first vertebral centrum. Individual bones of the skull, pectoral girdle, and pelvic girdle were compared simultaneously in all species, and measurements were made only when proportional differences were suspected. The only significant differences requiring measurements for definition were among those already pointed out by Godsil and Byers (1944) or Godsil and Holmberg (1950). Dial calipers were used in most cases, and articulation cartilages were removed from skull bones. The methods of mensuration follow.

Anterior articulating head of hyomandibula (See fig. 6). Length (B) was measured from the end of the horizontal articulation surface (pterotic head) to the most anterior point of the anterior articulation surface (sphenotic head). Least width (A) and greatest width were measured vertically on the anterior (sphenotic) head.

Metapterygoid (See fig. 7). The transition from anteroventral (C) to posteroventral (D) margin is usually an arc. Each margin was measured to the midpoint of the arc.

Quadrate (See fig. 8). Length (G) was measured from the most ventral part of the articular condyle to the tip of the spine. Width of horizontal edge (F) was measured along the horizontal dorsal edge to the point where it forms a slight depression before the spine. Total width (E) was measured from the anterior point of the horizontal dorsal edge along a projection of the line of this edge to the posterior margin of the spine.

36th vertebra. Length was measured along the axis of the centrum from the outer anterior rim to the outer posterior rim. Width was measured vertically on the lateral surface at the narrowest part of the centrum and does not include the neural or haemal arches.

Bone terminology is that of de Sylva (1955), which has been used for tuna osteology by most other recent workers. A number of names differ from those accepted by many fish osteologists.

PART 1. COMPARATIVE ANATOMY

The morphological characters useful for distinguishing the species of *Thunnus* fall into seven groups: osteology, viscera, vascular system, olfactory organ, meristic characters, morphometric characters, and coloration. These will be discussed in this order in this section of the paper. The first three groups, osteology, viscera, and vascular system, include the most important characters.

OSTEOLOGY

Osteological characters are very important in distinguishing species of *Thunnus*. They have an advantage over characters in the soft anatomy in that the bones can be saved so future workers can reexamine the material on which a study is based. We have used a large amount of the material Godsil and his co-workers reported on. Four groups of osteological characters will be considered: neurocranium, branchiocranium, pectoral and pelvic girdles, and vertebral column. The most useful characters are in the skull and the vertebral column. Each of the four groups will be discussed separately, giving a general osteological description followed by an enumeration of the specific characters.

Neurocranium

General characteristics.—Details of the general neurocranial structure of tunas have been illustrated by Masterman (1894), Kishinouye (1923), Frade (1932), Gregory (1933), Godsil and Byers (1944), de Sylva (1955), and Nakamura (1965). The accompanying labeled figures of an albacore (*Thunnus alalunga*) skull show the bones of the neurocranium (figs. 1–3). Photographs of the skulls of six of the seven species of *Thunnus* are presented in appendix figs. 1–3.

The skull of a tuna, compared with that of most typical percoid fishes, is short and wide. In dorsal view (fig. 2), at its anterior end, the dermethmoid (= ethmoid) is wide and its anterior margin only slightly curved. The interorbital region is broad, and the otic region broader still. A prominent dorsolateral crest is formed on each side by the frontal, parietal, and epiotic bones; each of the epiotics bears a short, posteriorly directed process. The lateral edges of the frontal and pterotic, making up the sides of the roof of the neurocranium, form a more prominent and rather flat sharp crest on each side which extends posteriorly as a long plate-like pterotic spine. The supraoccipital crest is high and extends posteriorly over the first few vertebrae.

Ventrally, the dentigerous vomer (= prevomer) is flanked by broad processes of the parethmoids (= lateral ethmoids). Most of the base of the skull is formed by the parasphenoid, which is flat or slightly concave in its anterior two-fifths, bears a medial, ventrally directed crest in the next two-fifths, and posteriorly is first convex, then deeply concave, with dorsomesially curved lateral flanges that enclose a parasphenoid chamber. Lateral wings project dorsad from near the end of the ventral crest to form part of the posterior myodome.

In lateral view, the alisphenoids (= pterosphenoids) form a partial interorbital septum extending ventrad from the roof of the skull. In extreme cases (large *Thunnus thynnus*) this septum may be fused with the parasphenoid, to form a bony septum partially separating the orbits. In the posterior part of the

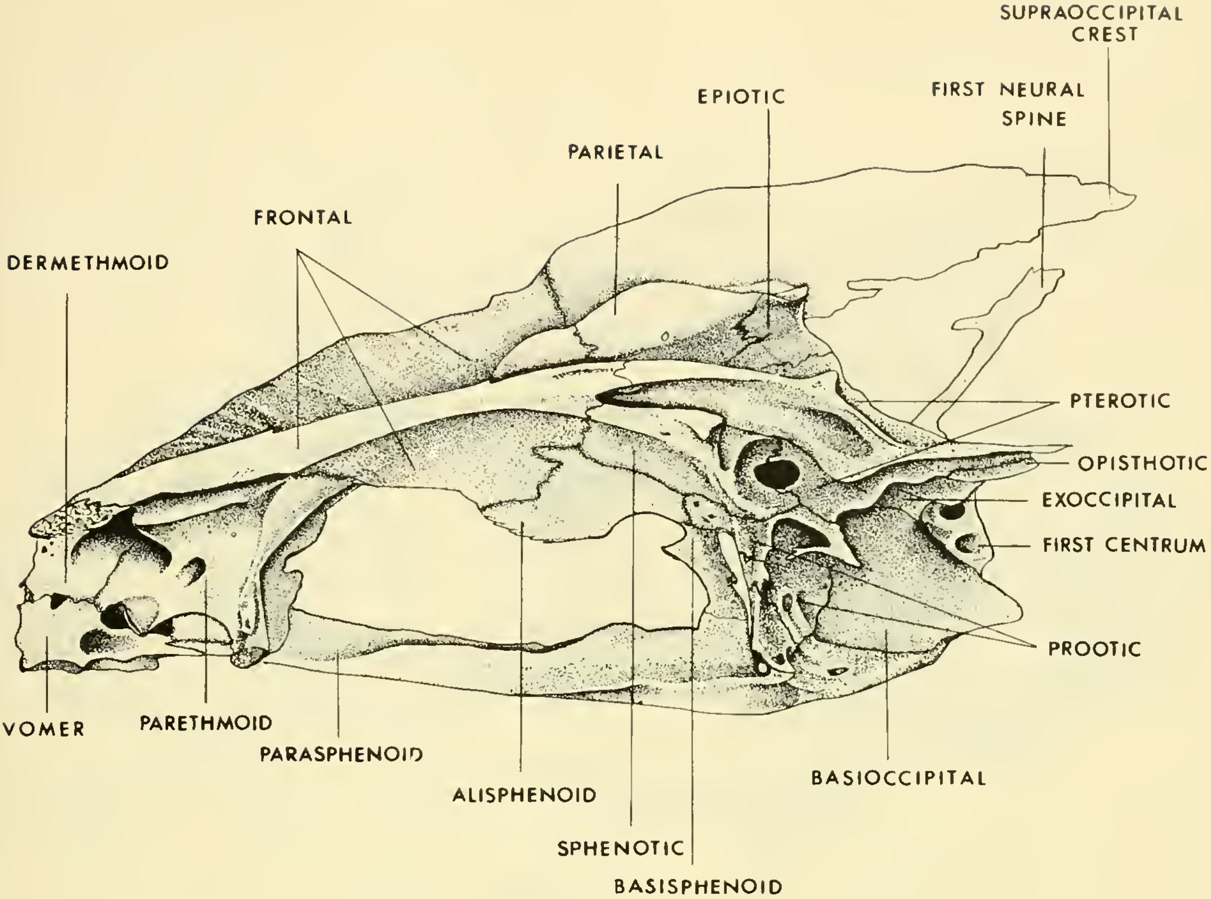

SUPRAOCCIPITAL CREST
EPIOTIC
FIRST NEURAL SPINE
PARIETAL
FRONTAL
DERMETHMOID
PTEROTIC
OPISTHOTIC
EXOCCIPITAL
FIRST CENTRUM
PROOTIC
VOMER
PARETHMOID
PARASPHENOID
ALISPHENOID
BASIOCCIPITAL
SPHENOTIC
BASISPHENOID

Figure 1.—Skull of *Thunnus alalunga*. Lateral view.

orbital region is a median, vertically oriented basisphenoid, which usually has an anteriorly directed process near its dorsal end. The posterior base of the cranium is formed by the end of the parasphenoid (ventral profile) and the lateral flanges of the basioccipital (posterior profile). The first vertebra articulates firmly, partly by a jagged suture, with the occipital region and forms an integral part of the skull. One end of Baudelot's ligament attaches to the basioccipital, the other end to the supracleithrum.

The prootic pits (Godsil, 1954) are large pouchlike concavities on each side of the ventral surface of the cranium, opening posteriorly and separating the pterotic bones from the brain case. Part of the roof, floor, and sides of each prootic pit is formed by the prootic bone, and the anterior wall by the sphenotic. The pits function as areas of attachment for the branchial musculature. These pits are characteristic of the most advanced scombrids—*Thunnus*, *Euthynnus*, *Katsuwonus*, *Auxis*, and *Allothunnus*—and are incipient in *Sarda* (Starks, 1910; Godsil, 1954).

The posterior myodome is a deep median depression opening anteriad at the posterior end of the orbital region. Its anterolateral walls and roof are formed by the prootics, its floor and ventrolateral walls by the parasphenoid, and its posterior concave wall by the basioccipital. The posterior myodome functions as a place of attachment for the rectus muscles of the eyes. The narrow basisphenoid lies just anterior to the anterior opening of the posterior myodome. There is a posterior or parasphenoidal chamber (Kishinouye, 1923), which communicates with the posterior myodome and is formed by the upcurved walls of the posteriormost end of the parasphenoid.

A large triangular fronto-parietal foramen (lateral parietal foramen of Masterman, 1894) is present on each side of the dorsal surface of the skull, at the junction of the frontal, parietal, and supraoccipital

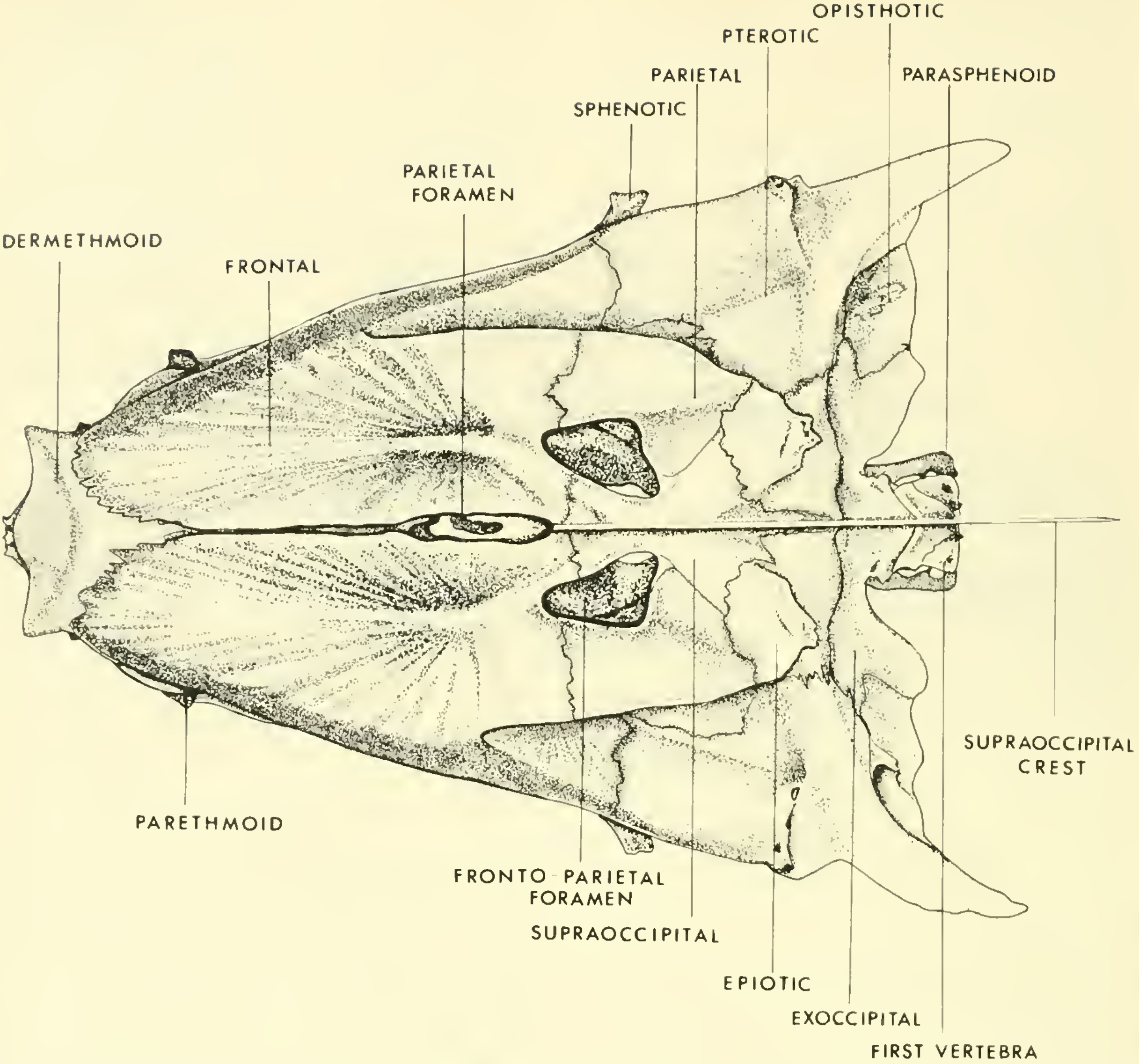
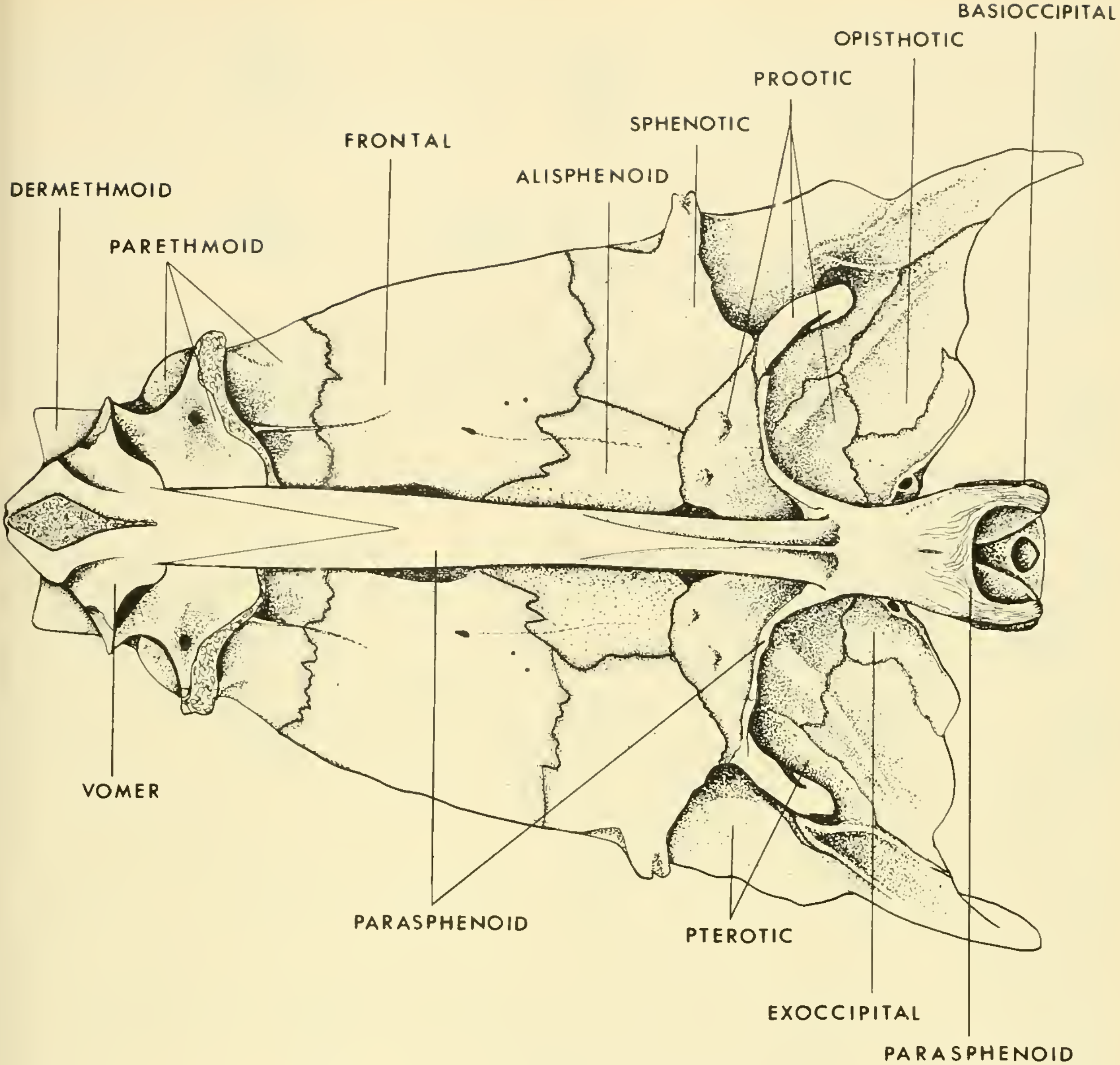

OPISTHOTIC
PTEROTIC
PARIETAL
PARASPHENOID
SPHENOTIC
PARIETAL FORAMEN
DERMETHMOID
FRONTAL
SUPRAOCCIPITAL CREST
PARETHMOID
FRONTO-PARIETAL FORAMEN
SUPRAOCCIPITAL
EPIOTIC
EXOCCIPITAL
FIRST VERTEBRA

FIGURE 2.—Skull of *Thunnus alalunga*. Dorsal view. [The pineal foramen is incorrectly labeled as parietal foramen.]

bones. In life these foramina are covered by a tough membrane and are not passages for nerves or blood vessels. We were unable to determine their function. Fronto-parietal foramina are characteristic of *Thunnus, Euthynnus,* and *Katsuwonus,* and the bone is thin in this area in several other scombrids.

There is a prominent medial pineal foramen between the edges of the frontal bones, just anterior to the supraoccipital crest. Rivas (1954a) has suggested that in *T. thynnus* light can pass through the transparent "window" in the skin over this foramen and then down to the brain through the cartilaginous lens that fills the foramen in life. He postulated that the pineal apparatus has a phototropic function involved in migration. Holmgren (1958) also studied the pineal apparatus of *T. thynnus* but could find no evidence of a photoreceptive role for the pineal organ. The pineal foramen is characteristic of the more advanced members of the Scombridae and is absent or represented by only a small slit in the more primitive genera such as *Scomber*, *Rastrelliger*, and *Scomberomorus* (Allis, 1903; Kishinouye, 1923; Mago Leccia, 1958).

Specific Characters.—Four neurocranial characters


BASIOCCIPITAL
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PROOTIC
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FRONTAL
ALISPHENOID
DERMETHMOID
PARETHMOID
VOMER
PARASPHENOID
PTEROTIC
EXOCCIPITAL
PARASPHENOID

FIGURE 3.—Skull of *Thunnus alalunga*. Ventral view.

have been found useful in distinguishing the species of *Thunnus:* the alisphenoids, posterior parasphenoid margin, supraoccipital crest, and ventral parasphenoid shaft. They are characteristic of specimens from all oceans.

Alisphenoids (fig. 4). The alisphenoids meet in the median line and extend ventrad into the orbit. They approach the parasphenoid more closely in *T. thynnus* and *T. maccoyii* than in the other tunas. The greatest height of the anterior part of the orbit, B, measured from dorsal parasphenoid to upper median part of parethmoid, was divided by the least distance between alisphenoid and parasphenoid, A. In 46 skulls of *T. thynnus*, 16 have the alisphenoids fused to the parasphenoids; in the remaining 30, A goes into B 2–15 times; with a mean ($\bar{x}$) of 4.8, only in 6 specimens is the ratio less than 2.5. No fusion was observed in *T. maccoyii;* in 17 skulls the ratio was 2.0-10.3, $\bar{x}$ 4.8. By contrast, in all other species, A goes into B 1–3 times. Among 122 skulls of the other species, only 3 *T. albacares* and 2 large *T. tonggol* have a ratio of 2.5 or greater. Mean

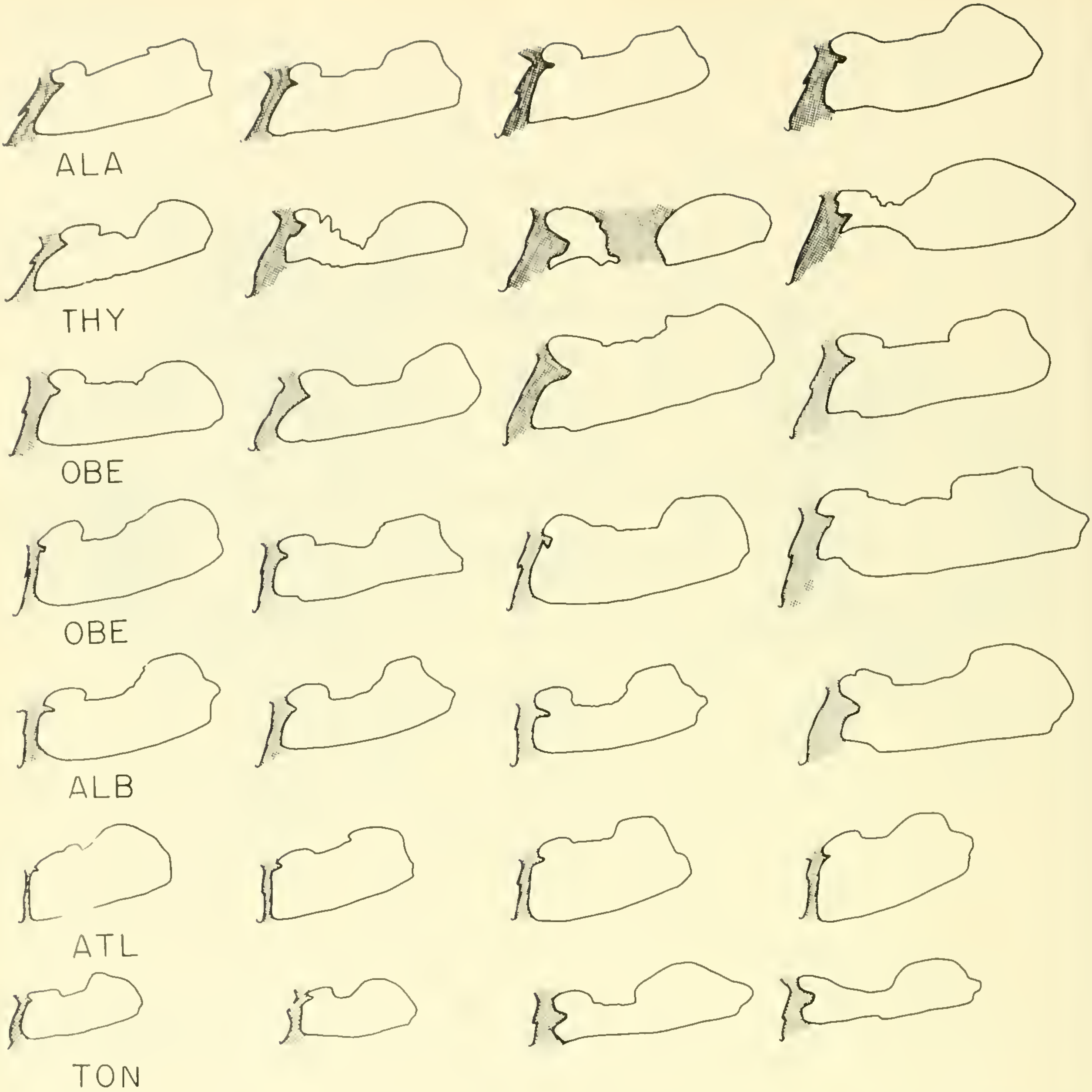


FIGURE 4.—Skulls of *Thunn* [illegible] Right lateral view of orbital region of neurocranium showing conformation of basisphenoid (stippled) and al[illegible]d. Arrangement within each species in order of increasing skull lengths from left to right: ALA—*T. alalunga*, 131, 138, 150, 167 mm. ALB—*T. albacares*, 103, 116, 122, 179 mm. ATL—*T. atlanticus*, 51, 80, 97, 102 mm. OBE—*T. obesus:* upper-Atlantic, 170, 181, 185, 207 mm.; lower-Pacific, 97, 142, 147, ca. 240 mm. THY—*T. thynnus*, 76, 139, 231, ca. 320 mm. TON—*T. tonggol*, 57, 61, 122, 128 mm.

values are: *T. tonggol* ($N=8$) 2.0; *T. albacares* ($N=43$) 1.8; *T. obesus* ($N=32$) 1.6; *T. alalunga* ($N=27$) 1.6; *T. atlanticus* ($N=14$) 1.2.

Posterior parasphenoid margin (fig. 5). The portion of the parasphenoid forming the walls of the parasphenoidal chamber is partially covered laterally by the basioccipital. Together the margins of these bones extend ventrad from the first vertebra, either vertically or slanting forward or backward; anteriorly the parasphenoid alone forms the margin. With due consideration for growth changes and individual variation, the profile formed at this part of the skull

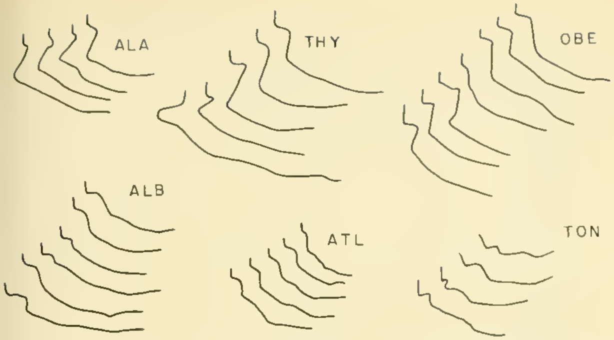


FIGURE 5.—Skulls of *Thunnus* species. Right lateral view of posteroventral part of neurocranium showing conformation of posterior parasphenoid margin. Arrangement within each species in order of increasing skull length from right to left. ALA—131, 138, 150, 167 mm. ALB—103, 107, 116, 122, 169, 179 mm. ATL—51, 80, 88, 97, 102 mm. OBE—Pacific, 97, 141, 143, 146, 165, 189, 210 mm. THY—76, 139, 230, 335 mm. TON—57, 61, 122, 127 mm.

is quite characteristic of some species.

In *T. thynnus*, *T. maccoyii*, and *T. alalunga* a decided angle is formed by the posterior parasphenoid margins. The acuity of the angle and its posterior extent generally increase with size in *T. thynnus* (fig. 5), and extreme development of the angle is found in very large specimens. Within its observed size range (skull length 88–167 mm.), *T. alalunga*, however, displays a more acute angle than does *T. thynnus* of similar size. *T. maccoyii* resembles *T. thynnus* in this respect.

In relatively large specimens of *T. obesus* the angle is apparent but not as acute as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*. Observations of Pacific specimens indicate probable changes with growth. The two smaller eastern Pacific specimens reported by Godsil and Byers (1944) and again by de Sylva (1955) have rounded margins, but other eastern Pacific specimens within the same size range show a definite angle.

T. albacares, *T. atlanticus*, and *T. tonggol* exhibit great variation. Some have unmistakably rounded margins; others are somewhat angulate but have a very short distance from the first vertebral centrum to the apex of the angle, so that the angle itself is never obvious.

Supraoccipital crest. In *T. alalunga* (fig. 1) the supraoccipital crest is relatively more slender than in any of the other species of *Thunnus* and is longer, nearly always reaching at least to the centrum of the third vertebra. In the other six species the crest rarely extends beyond the second vertebra.

Ventral parasphenoid shaft. In *T. atlanticus* the anterior portion of the parasphenoid shaft is concave ventrally (de Sylva, 1955). In *T. tonggol* we found it concave in three small specimens (skull length 57–99 mm.) and flat in two larger specimens (skull length 122–128 mm.). It is most commonly flat or slightly convex in the other species, but a degree of concavity has been observed in individuals, especially young, of all except *T. obesus*.

Other characters.—Godsil and Byers (1944) cited several additional neurocranial characters that are supposedly useful in distinguishing among the species. In our estimation, none of these is valid for the following reasons.

The parietal crest in *T. albacares* was described as extending farther forward than in *T. obesus* so that a projection of the curvature of the lateral edge of the parethmoid (prefrontal of Godsil and Byers) would be continuous with the parietal crest in *T. obesus* but would run below it in *T. albacares*. Our material shows both conditions in all species.

The angle of the long axis of the basisphenoid relative to the parasphenoid is highly variable and not reliable as a specific character. The width of the basisphenoid relative to its height is not only variable within any given size range but also changes with growth.

The anteriorly directed process at the upper end of the basisphenoid was used by de Sylva as a distinguishing character (1955: 32–35). He described the process in *T. albacares* and *T. "sibi"* (Pacific *T. obesus*) as being directed obliquely ventrad so that a line drawn through its axis would transect the parasphenoid at or behind the junction with the parethmoid; in *T. thynnus*, *T. alalunga*, and *T. atlanticus* such a line would more nearly parallel the parasphenoid and would not cross it. We find this character variable within a species. Furthermore, in larger fishes, the entire bone becomes relatively shorter and wider, whereas, the process becomes broader and more rounded.

The head of the vomer in *T. alalunga* was described as having a thin bony ridge behind the dentigerous anterior portion, a similar ridge being present in some *T. thynnus*, but not in *T. albacares* or *T. obesus*. Actually, all the species may have such a ridge. In *T. alalunga* teeth are generally restricted to the anterior end; the posterior end is very thin. The other species usually, but not always, bear teeth along the entire ridge, and the posterior portion is wider. In *T. atlanticus* the ridge is usually absent.

These tendencies exist, but frequent exceptions render the character uncertain.

A depression in the dorsal profile just anterior to the supraoccipital, reported to be present in all species but most pronounced in *T. thynnus*, is related to the pineal foramen. We find this variable in all species and distinctive in none.

In the contour of the posterior margin of the sphenotic as seen in ventral view, we can detect no difference among the species. A concave curvature of the margin, held by Godsil and Byers to be characteristic of *T. alalunga* and *T. thynnus*, is not only slight but may be present or absent in all species.

Branchiocranium

General description.—The branchiocranium includes the branchial bones, opercular apparatus, jaws, and associated bones. On each side the dentigerous premaxilla forms the upper jaw, and the maxilla is located dorsomesial to it. A small supramaxilla is attached to the posterior end of each maxilla. The lower jaw includes the dentary, which bears teeth; the articular, forming the rear end of the jaw and articulating with the condylar region of the quadrate; and a small angular at the posteroventral corner of the articular. The suspensorium begins with the hyomandibula, which articulates at its upper end with the otic region of the neurocranium and with the opercle. The ventral limb of the hyomandibula articulates with the metapterygoid, and the ventral portion of the latter in turn articulates with the symplectic and quadrate. To the anteroventral part of the metapterygoid are joined the basal portions of the endopterygoid and ectopterygoid. At their anterior ends, these are joined to the short, dentigerous palatine, which articulates with the condyle of the anterior end of the maxilla.

In addition to the hyomandibula, the hyoid arch is composed of two median and four paired bones. A glossohyal supports the tongue, and a urohyal lies below and between the two sides of the arch. The paired bones include small basihyals, large ceratohyals that articulate with smaller epihyals by jagged, toothlike sutures on the mesial side only, and small interhyals posteriorly joining the operculum.

In the branchial arches are three median basibranchials (a small cartilage posterior to the third may represent a fourth basibranchial, see Iwai and Nakamura, 1964a) and on each side three hypobranchials, five ceratobranchials, four epibranchials, and four pharyngobranchials. The posteriormost ceratobranchials and mesial three pairs of pharyngobranchials bear villiform teeth. The anterior surfaces of the first four arches bear gill rakers, and, as supports for the gill filaments, so-called gill bars are found on the posterior surfaces (Iwai and Nakamura, 1964a).

Specific Characters.—Differences worthy of note have been described for only six bones by Kishinouye (1923) or Godsil and Byers (1944). These are the hyomandibula, metapterygoid, quadrate, subopercle, interopercle, and ceratohyal. We concur in their observations on the first four only.

The anterior (sphenotic) articulating head of the hyomandibula (fig. 6) is relatively longer and narrower in *T. alalunga* than in the other species. The proportion of length to least width in our specimens ranged as follows: *T. alalunga* ($N=35$) 1.7–2.7, $\bar{x}=2.2$; *T. thynnus* ($N=44$) 1.3–2.1, $\bar{x}=1.7$; *T. maccoyii* ($N=17$) 1.6–2.3, $\bar{x}=1.9$; *T. obesus* ($N=36$) 1.3–1.9, $\bar{x}=1.5$; *T. atlanticus* ($N=18$) 1.3–2.2, $\bar{x}=1.7$; *T. albacares* ($N=58$) 1.2–1.9, $\bar{x}=1.6$; *T. tonggol* ($N=4$) 1.4–1.8, $\bar{x}=1.6$. These proportions are close to those given by Godsil and Byers (1944: 86), who reported 1.7–3.0 for Pacific *T. alalunga* and 1.2–1.5 for Pacific *T. albacares*, and stated that Pacific *T. thynnus* and *T. obesus* are similar to *T. albacares*.

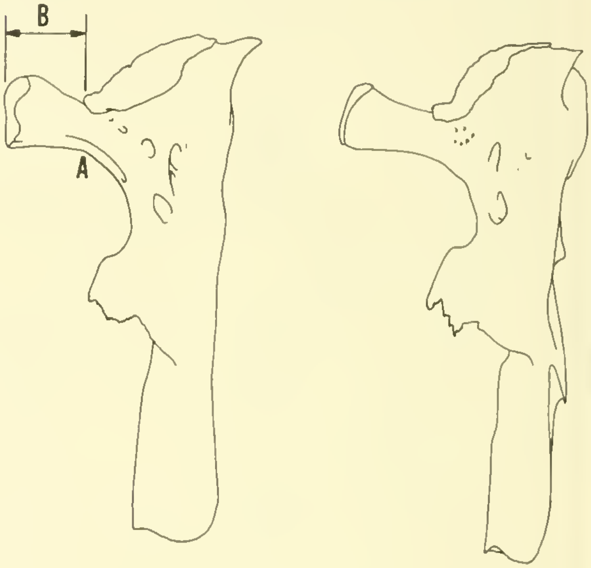


Figure 6.—Hyomandibula of (left) *Thunnus thynnus*, skull length 139 mm., (right) *T. alalunga*, skull length 150 mm. Measurements of anterior articular head include A—least width, B—length.

Kishinouye (1923: 322) stated that the anterior head is "more or less roundish in cross-section in *Thunnus;* but more or less flattened in *Parathunnus* and *Neothunnus*. . . ." We can find no significant difference among any of the species in this character. Furthermore, we cannot confirm de Sylva's contention (1955:14) that the process is oblique to the vertical limb in *T. atlanticus* but forms a right angle in the other species.

In *T. alalunga* the metapterygoid (fig. 7) is narrower than in other species. This condition can be indicated by the proportion of the length of the anteroventral margin to the posteroventral margin (measured in each case to the midpoint of the arc of the posteroventral edge.) In our material, this proportion is as follows: *T. alalunga* ($N=32$) 1.1–1.8, $\bar{x}=1.4$; *T. thynnus* ($N=43$) 1.6–2.6, $\bar{x}=2.0$; *T. maccoyii* ($N=17$) 1.4–2.7, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.5–3.1, $\bar{x}=2.0$; *T. atlanticus* ($N=19$) 1.4–2.1, $\bar{x}=1.7$; *T. albacares* ($N=58$) 1.5–3.1, $\bar{x}=2.1$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. These proportions are similar to those given by Godsil and Byers (1944: 86) for Pacific tunas, but provide even better distinction. Godsil and Byers measured each margin to the "most ventral point," which seemed more nebulous to us than the midpoint of the arc. Their figures of 1.0–1.5 for *T. alalunga* and 1.3–1.9 for *T. albacares* and the other species include slightly lower proportions than were found in our specimens, but the conclusions are nevertheless similar.

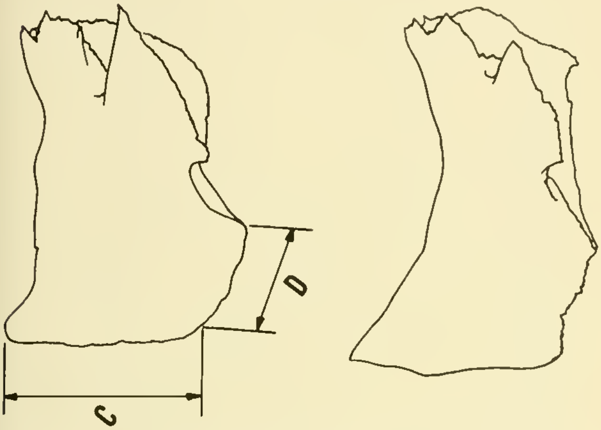


FIGURE 7.—Metapterygoid of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of C—anteroventral margin, D—posteroventral margin.

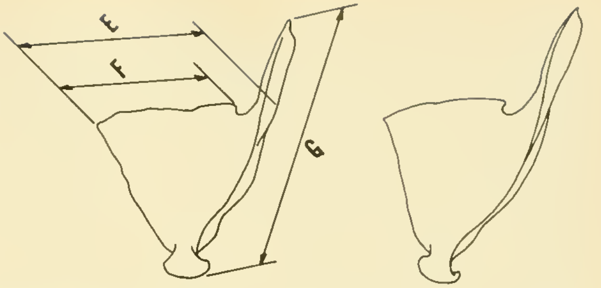


FIGURE 8.—Quadrate of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of E—total width, F—width of horizontal edge, G—length.

Again, in *T. alalunga* the quadrate (fig. 8) is slightly narrower than in the other species. The proportion of length to total width in our specimens is as follows: *T. alalunga* ($N=35$) 1.5–2.1, $\bar{x}=1.8$; *T. thynnus* ($N=44$) 1.2–1.6, $\bar{x}=1.4$; *T. maccoyii* ($N=16$) 1.3–1.5, $\bar{x}=1.4$; *T. obesus* ($N=37$) 1.4–1.7, $\bar{x}=1.5$; *T. atlanticus* ($N=20$) 1.3–1.8, $\bar{x}=1.6$; *T. albacares* ($N=57$) 1.4–1.8, $\bar{x}=1.5$; *T. tonggol* ($N=4$) 1.4–1.6, $\bar{x}=1.5$. The proportions of the same length to width of the horizontal dorsal edge are: *T. alalunga* ($N=35$) 2.1–2.7, $\bar{x}=2.5$; *T. thynnus* ($N=44$) 1.6–2.1, $\bar{x}=1.9$; *T. maccoyii* ($N=16$) 1.6–2.0, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.8–2.2, $\bar{x}=2.0$; *T. atlanticus* ($N=20$) 2.0–2.3, $\bar{x}=2.1$; *T. albacares* ($N=57$) 1.8–2.2, $\bar{x}=2.0$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. We are not certain where Godsil and Byers (1944: 87) measured the width, but they gave proportions of 1.8–2.3 for Pacific *T. alalunga* and 1.6–1.8 for other species. Thus there is agreement in order of magnitude, but their proportions are generally higher than our first and lower than our second.

The subopercle of *T. thynnus* and *T. maccoyii* (fig. 9) differs, with few exceptions, from that of the other species in being relatively narrow and in having the anterodorsal margin almost vertical in its lower two-fifths to one-half, followed by a decided change in slope of the upper portion. In the other species there may be a very short perpendicular portion, less than one-fifth of the length, before the oblique slope begins, or, most often, there is an almost straight or very slightly convex oblique edge. This finding conforms with the observations of Godsil and Byers (1944: 101) for the Pacific forms and presumably also with the observations of Kishinouye (1923: 325), although his statement is less clear.

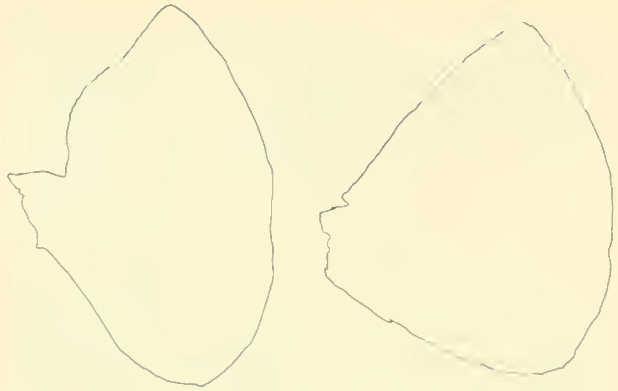


FIGURE 9.—Subopercle of (left) *Thunnus thynnus*, (right) *T. alalunga*. Same specimens as in fig. 6.

We are unable to confirm two other characters mentioned by Kishinouye (1923: 325, 327). In Japanese *T. thynnus* the posterior margin of the interopercle was described as being convex, whereas in other Japanese tunas it is nearly straight. In our material the shape of the margin is variable; most of the species have both types and variants thereof. Kishinouye also described a groove for blood vessels along the dorsolateral edge of the ceratohyal. The groove was present in *T. thynnus*, *T. alalunga*, and *T. obesus* but hardly visible in *T. albacares*. This grove is present in all species and is generally more apparent in larger specimens. In small specimens of most species the groove is indistinct or absent.

Pectoral and Pelvic Girdles

The pectoral girdle is composed of a series of bones connecting the skull and the pectoral fin. The two-armed supratemporal, not really a functional part of the pectoral girdle, is closely applied to the skin beside the otic region of the neurocranium. A larger, also two-armed, posttemporal articulates with the skull, followed by a supracleithrum and the large, curved, bladelike cleithrum. Baudelot's ligament runs from the supracleithrum to the basioccipital. From the posterior margin of the supracleithrum extend two flattened postcleithra, the second of which has an attenuated posteriorly directed process. The long curved blade of the cleithrum forms a thin-walled trough that opens posteriorly. The thickened, somewhat rectangular scapula is borne dorsally, on the mesial side. Below the scapula, the bladelike coracoid is attached. The lower, posterior end of the scapula and the uppermost posterior edge of the coracoid are thickened and flattened; they form articular surfaces for four pterygials, on which the fin rays are borne.

The pelvic girdle includes a pair of winglike basipterygia that join posteriorly in the median line. Anteriorly each bone has a flattened lateral wing and a long narrow mesial process. Posteriorly a long mesial process extends between the fin rays. There are no pterygials.

No differentiating characters are apparent in either the pectoral or the pelvic girdle.

Vertebral Column

General description.—Important papers describing the vertebral column in species of *Thunnus* include: Starks (1910), Kishinouye (1923), Frade (1932), Godsil and Byers (1944), Godsil and Holmberg (1950), Clothier (1950), de Sylva (1955), and Nakamura (1965).

The vertebral column usually has 39 vertebrae, including the hypural plate. The first vertebra is articulated firmly with the rear of the skull. Neural arches and spines are present on all except the hypural plate. The spines are erect and laterally flattened on the first six vertebrae. On the seven vertebrae anterior to the hypural plate, both the neural and haemal spines are wide and depressed and lie on top of the next posterior centrum, forming a strong and rigid tail section. Laterally directed transverse processes (parapophyses) appear as small projections on the third vertebra, become longest and broadest on about the sixth, shorter and more canted on the next two or so, and usually become both longer and ventrally directed on the eighth or ninth. By the 10th or 11th vertebra, the first closed haemal arch is formed by the meeting of the distal ends of the parapophyses. The ventral ends of the haemal arches become progressively longer, forming haemal spines. Ribs are attached, beginning with the 3d vertebra, to each parapophysis or to the end of each haemal arch or spine until the 18th or 19th vertebra. Posteriorly, haemal spines are present, but ribs are absent. Dorsal to the ribs, intermuscular bones (epipleurals) articulate either on the neural arch or the centrum of each of the vertebrae from the 1st to the 31st.

Beginning at the 12th to 18th vertebra, each haemal arch bears on each side a process directed obliquely ventrad which has been called a haemal prezygapophysis (de Sylva, 1955). On succeeding vertebrae this process is longer, then shorter and more dorsally situated; by the 20th to 25th vertebra it comes to arise from the anterior end of the centrum rather than from the haemal arch.

Beginning at about the fourth vertebra, a process which has been called a haemal postzygapophysis (de Sylva, 1955) arises on each side from the posterior end of each centrum. On the anterior centra it is small and laterally directed. This process becomes ventrally directed on the eighth vertebra, and its distal end meets the parapophysis; farther posteriorly it meets the upper part of the haemal arch or the haemal prezygapophysis when it is formed. On approximately the last eight vertebrae the haemal spines are situated so posteriorly that they obliterate the haemal postzygapophyses.

From some or all of the 20th to the 33d vertebrae, the blood vessels and nerves that emerge from the haemal canal exit through ventrolateral foramina. The anterior foramina are formed by struts running from the haemal arch to the centrum near the base of the haemal postzygapophyses. They become smaller posteriorly and are separate from and anterior to the haemal arches; the latter in this region gradually become located toward the posterior end of the centra. On the 32d to 36th vertebrae, flattened lateral processes form a horizontal bony keel. The sizes of the individual vertebrae vary considerably, and regional differences are emphasized in older specimens. The length increases regularly to the 35th vertebra; the 36th is slightly shorter, the 37th and 38th are very short, and the 39th is incorporated into the wide, triangular hypural plate. The depth of the vertebra increases regularly to about the 25th, beyond which there is a gradual decrease to the hypural plate. A simple splintlike bone (epural) is closely applied to the anterodorsal surface of the hypural plate. A similar bone (hypural) bearing a spinous process on each side is present along the anteroventral surface of the hypural plate. The terminology and derivation of these two bones are in doubt.

Specific Characters.—The vertebrae typically total 39 in all species. Godsil and Byers (1944) reported, and we have reexamined, a California *T. thynnus* with only 38, in which 1 vertebra near the hypural is obviously missing. Among more than 200 skeletons of the seven species, we found only three additional abnormalities, all due to recognizable fusion of two adjacent centra. Frade (1932) reported, among 110 *T. thynnus*, 8 with 38 vertebrae, 6 with 40, and 1 with 41. We doubt the counts of 40 and 41 but cannot explain them. All but one species have 18 precaudals and 21 caudals, the first long haemal spine occurring on the 19th vertebra. The same count was given by de Sylva (1955) for *T. atlanticus*, but, as Watson (1964) has shown, this species differs from all other *Thunnus* in having 19 precaudals and 20 caudals. Exceptions may be expected in all species; we have examined *T. atlanticus* with counts of 18+21 and 20+19, *T. obesus* and *T. albacares* with 17+22, and *T. thynnus* and *T. obesus* with 19+20; and Godsil and Byers (1944: 86) reported one *T. alalunga* with 20+19.

The position of the first (anteriormost) ventrally directed parapophyses appears to show almost no variability within a species or subspecies; only one exception has been noted. These parapophyses occur on the 8th vertebra in *T. thynnus*, on the 10th in *T. tonggol*, and on the 9th in the other species. In *T. alalunga* none of the parapophyses is directed quite so obviously ventrad as in the other species; those on the ninth vertebra that we regarded as ventrally directed are much shorter than in any other species and seem almost twisted, never becoming completely ventrally oriented. In other species, there is variation in the ventral extent of the preceding parapophyses. As long as these were more or less flattened and rounded, their relative location was not considered. The first ventrally directed ones are definitely elongated in a ventral direction (compare the eighth vertebra in *T. thynnus* and *T. maccoyii*, fig. 10).

The first (closed) haemal arch usually occurs on the 11th vertebra in *T. albacares*. *T. atlanticus*, *T. tonggol*, and *T. obesus*, and usually on the 10th vertebra in *T. alalunga*, *T. maccoyii*, and *T. thynnus*. In all species except *T. alalunga* and *T. maccoyii* we observed the first closed arch occasionally either one vertebra anterior or one vertebra posterior to the usual position. Godsil and Byers (1944: 68, 101) observed notable variation in Pacific *T. albacares* and in *T. thynnus*. In most of the species the parapophyses on the vertebra preceding the one that bears the first haemal arch approach each other so closely in the median line that it appears to be a matter of chance whether or not they or the next pair fuse. In many specimens in which the haemal arch was formed anterior to its usual position, its shape was noticeably different (fig. 10, OBE).

In *T. alalunga* the first haemal arch is directed forward, with an angle of about 45° or less between it and the vertebral axis. In all of the other species

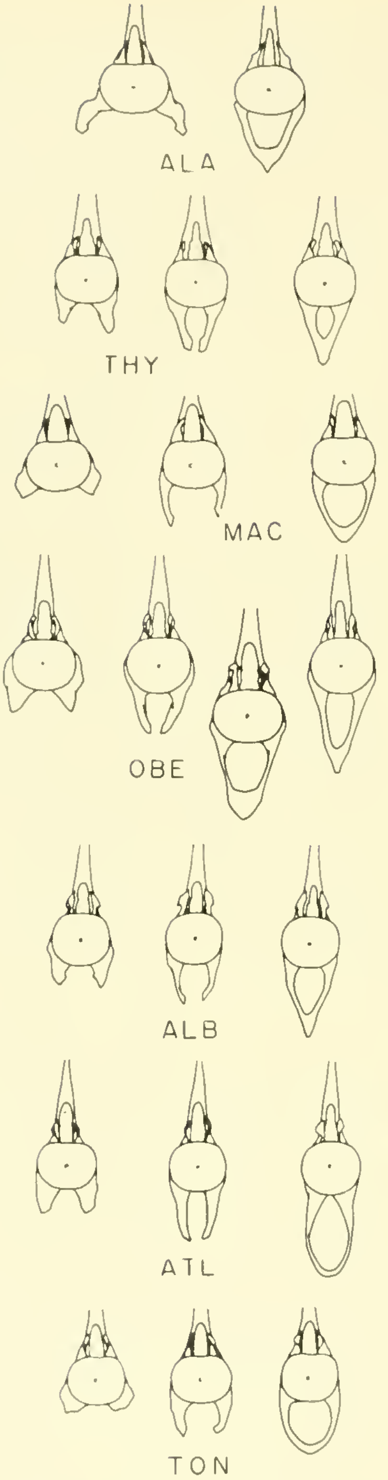


FIGURE 10.—Anterior view, first closed haemal arch and preceding vertebrae of *Thunnus* species. ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, MAC—8–10, OBE—9–11 (the one slightly below the main row shows shape of first closed haemal arch when located on 10th vertebrae), THY—8–10, TON—9–11.

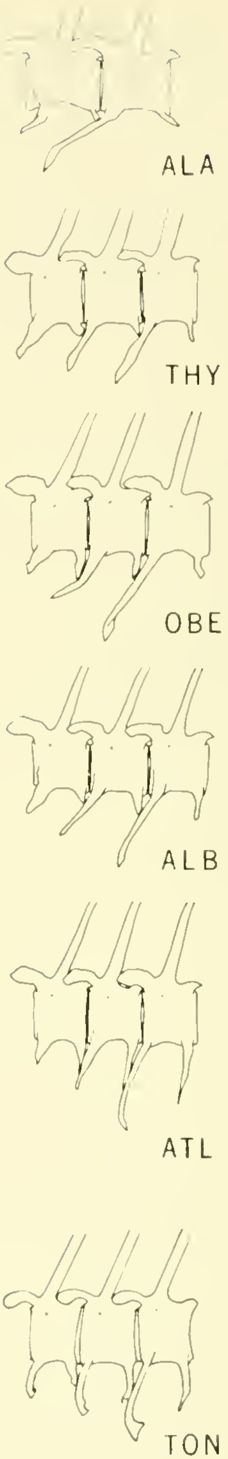


FIGURE 11.—Left lateral view of vertebrae of *Thunnus* species showing first ventrally directed parapophyses (left vertebra) and first closed haemal arch (right vertebra). ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, OBE—9–11, THY—8–10, TON—10–12.

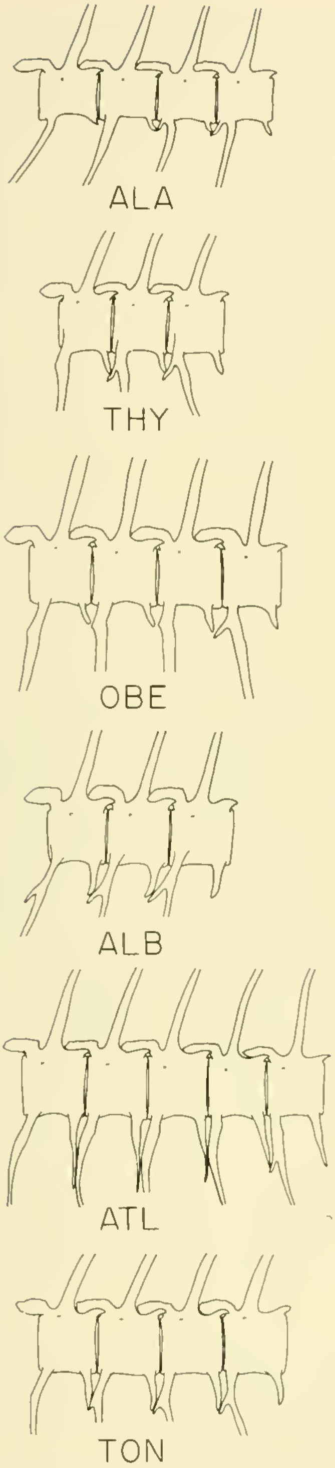


Figure 12.—Left lateral view of vertebrae of *Thunnus* species, showing development of anteriormost haemal pre- and postzygapophyses. ALA—vertebrae 13–16, ALB—14–16, ATL—14–18, OBE—14–17, THY—14–16, and TON—14–17.

it may range from almost perpendicular to a 60° angle (fig. 11). The shape of the first haemal arch and the dimensions of its bony parts vary considerably, but in *T. atlanticus, T. tonggol,* and *T. maccoyii* the bony portions are thinner and the sides more bowed than in the other species (fig. 10).

As shown by Yabe et al. (1958), by Matsumoto (1963), and by Yoshida (1965), the heamal spine of the first caudal vertebra is always laterally flattened and winglike in *T. alalunga* but in the other species resembles the other haemal spines and is not flattened.

The length of the haemal prezygapophyses and the distance of their origin from the centrum vary among the species of *Thunnus.* In *T. alalunga* the haemal prezygapophyses all originate at the centrum or extremely close to it. Correlated with this, the anterior haemal postzygapophyses are relatively short (fig. 12). In the other species the anterior haemal prezygapophyses arise from the sides of the haemal arches of 3 to 12 vertebrae before they begin to arise from the centra, and the posterior haemal postzygapophyses are relatively longer. In *T. alalunga*, *T. obesus*, *T. maccoyii*, and *T. thynnus* the haemal prezygapophyses arise high on the neural arch, so that only the first two or three at most can be regarded as clearly on the arch. Correspondingly, the associated haemal postzygapophyses hardly differ in length from those on the posterior vertebrae. By contrast, in *T. atlanticus*, *T. albacares*, and *T. tonggol* the haemal prezygapophyses arise far more ventrad on the haemal arch, from one-fourth to one-half the distance to the ventral tip, and there is no question that at least five (usually more) are definitely on the arch, not on the centrum. The associated haemal postzygapophyses in these species are longer than in the other three, although less so in *T. albacares* than in *T. atlanticus* and *T. tonggol.* In *T. atlanticus* and *T. tonggol* the longest haemal postzygapophyses are equal to or longer than the length of the centra; in *T. albacares* they may be about three-fourths the centrum length.

The species differ in the development of the ventrolateral foramina that are found on some or all of the 20th to the 33d vertebrae (fig. 13). These foramina are best developed anteriorly and in this region appear to arise through the formation of a bony strut from the haemal postzygapophyses to the dorsal part of the haemal arch. They diminish in size posteriorly and are absent on the last several vertebrae. In *T. atlanticus, T. albacares,* and *T. tonggol* the anterior openings are large, longer than wide,

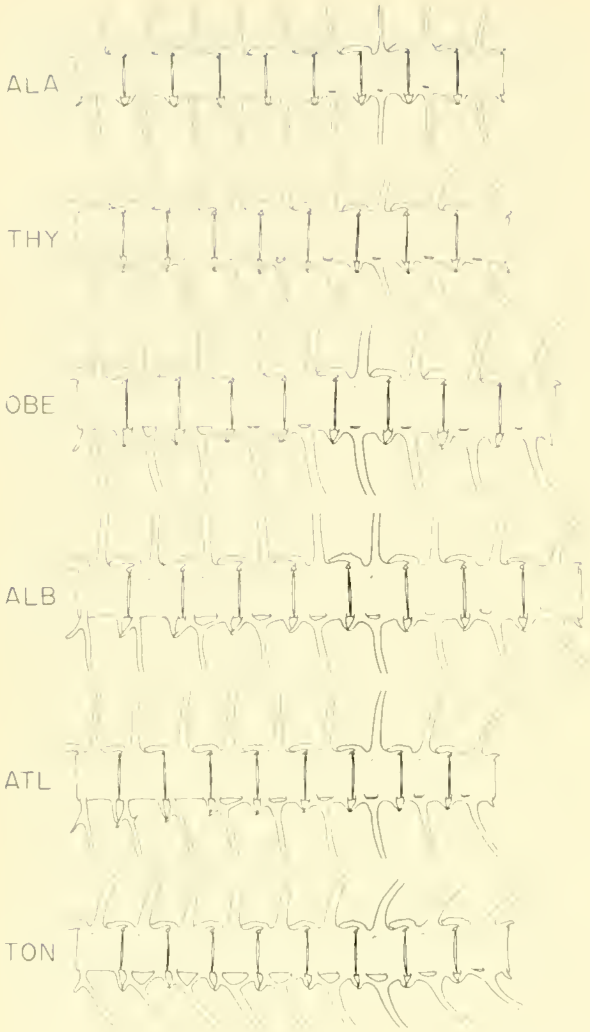


Figure 13.—Left lateral view of vertebrae 20–28 of *Thunnus* species, showing development of inferior foramina.

the largest usually three times or more as long as the horizontal width of the base of the corresponding haemal spine. In *T. obesus, T. maccoyii, T. thynnus,* and *T. alalunga* the size of the openings is variable, usually small, and the largest opening is rarely more than about 1.5 times as long as the width of the adjoining bony neural arch.

T. atlanticus, T. albacares, and *T. tonggol* are distinguishable by the development of vertebral processes and openings, which approach the ornate trelliswork seen in *Auxis, Euthynnus,* and *Katsuwonus; T. alalunga* shows the least development, and *T. obesus, T. maccoyii,* and *T. thynnus* are intermediate.

The first haemal prezygapophysis tends to be found more anteriorly in *T. albacares* and *T. tonggol,* most commonly on vertebra 13 or 14 (range 12–15) in *T. albacares.* In *T. maccoyii* it usually occurs on 14 or 15 (range 14–16), in *T. alalunga* and *T. obesus* on 15 or 16 (range 14–17), and in *T. atlanticus* on 16 or 17 (range 15–18). *T. thynnus* displays a wider range of variation (12–17), and overlap is considerable between it and the other species.

While this paper was in press, Nakamura and Kikawa (1966) described specific differences in the infra-central grooves on the ventral side of the centra of vertebrae 10-30. These infra-central grooves were categorized into three types: type A with two separate infra-central grooves; type B with two grooves connected by a canal; type C with a single, usually elongate, groove. We have reexamined our skeletal material, which comprises many more specimens than the total of 19 used by Nakamura and Kikawa, and we conclude that the infra-central grooves are a useful character, but show variation that often precludes positive species identification. Our conclusions are as follows:

Thunnus albacares (24 specimens, fork length 280-1,430 mm.) has type C infra-central grooves that tend to be divided by a thin septum anteriorly but that posteriorly are undivided or occupied by a honeycomb-like network of bony material. In this character, *T. albacares* is distinctive, but is approached by some specimens of *T. maccoyii.*

Thunnus maccoyii (16 specimens, 742-1,445 mm.) is the most variable of all the species. Very few have type C (undivided) grooves, as described by Nakamura and Kikawa. Typically, all the vertebrae have two grooves (type A) that are divided by very thin septa or a honeycomb of septa. This condition resembles that of the anterior grooves of *T. albacares.* Only an occasional undivided groove occurs among the divided ones in *T. maccoyii,* whereas most of the grooves are undivided in *T. albacares.* Some specimens, particularly the six from Australia that were used by Godsil and Holmberg (1950), were almost impossible to distinguish from *T. thynnus.*

Thunnus thynnus thynnus (7 specimens, 316-2,315 mm.) and *T. t. orientalis* (18, 530-1,450 mm.) have type A grooves, two grooves per centrum, that tend to be round or oval anteriorly and become longer and narrower posteriorly. The distance between the two grooves on the anterior centra is highly variable. When the grooves are narrowly separated, the specimens resemble some *T. maccoyii.*

Thunnus obesus (7 Atlantic specimens, 697-1,360 mm.; 3 Indian Ocean, 630-1,270 mm.; 1 eastern Pacific, 1,600 mm.) have type A grooves and could not be distinguished from *T. thynnus.*

Thunnus alalunga (20 specimens, 520-1250 mm.), like *T. thynnus* and *T. obesus,* have type A grooves, but, although the grooves vary greatly in width, they tend to be much narrower than in the latter two species. Usually the grooves are widely separated, but in a few specimens, the partitions are narrow.

Thunnus tonggol (4 specimens, 373-924 mm.) have type B grooves, two grooves per centrum, quite variable in size, with a shallow canal connecting them. The grooves tend to be larger than those of *T. atlanticus* and smaller than those of *T. thynnus* or *T. obesus.* In the two larger specimens, the anterior grooves strongly resemble those of *T. thynnus* or *T. obesus* in being larger and close together.

Thunnus atlanticus (20 specimens, 322-665 mm.) have type B grooves, with two very small pits on each centrum connected by a very narrow canal. The canal is not evident in some specimens, giving the impression that the two grooves are separated by a sharp ridge. In this respect *T. atlanticus* is distinctive. The largest specimens, however, closely resemble small *T. tonggol,* with small grooves connected by an obvious canal, the grooves becoming elongate posteriorly.

The proportion of length to depth of the 36th vertebra is relatively greatest in *T. albacares* ($N=60$) 1.2–1.9, $\bar{x}=1.4$ and in *T. alalunga* ($N=40$) 1.1–1.7, $\bar{x}=1.5$. In *T. alalunga* the vertebrae are often considerably smaller anteriorly than posteriorly (fig. 14), accounting for the high ratio. In the other species, this proportion is: *T. thynnus* ($N=58$) 0.8–1.3, $\bar{x}=1.1$; *T. maccoyii* ($N=16$) 0.8–1.3, $\bar{x}=1.0$; *T. obesus* ($N=30$) 0.9–1.4, $\bar{x}=1.2$; *T. atlanticus* ($N=23$) 1.0–1.4, $\bar{x}=1.3$; *T. tonggol* ($N=8$) 1.1–1.5, $\bar{x}=1.3$.

VISCERA

The relative position, shape, and size of the various internal organs provide excellent diagnostic characters (fig. 15). These organs are treated here by systems. Important works on the viscera of *Thunnus* include those of Eschricht and Müller (1837), Kishinouye (1923), Frade (1925), Serventy (1942), Godsil and Byers (1944), and Godsil and Holmberg (1950).

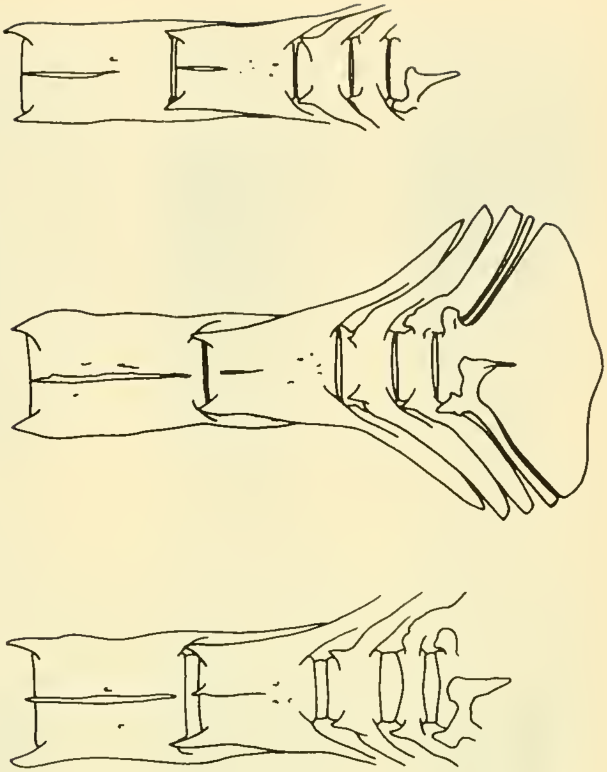
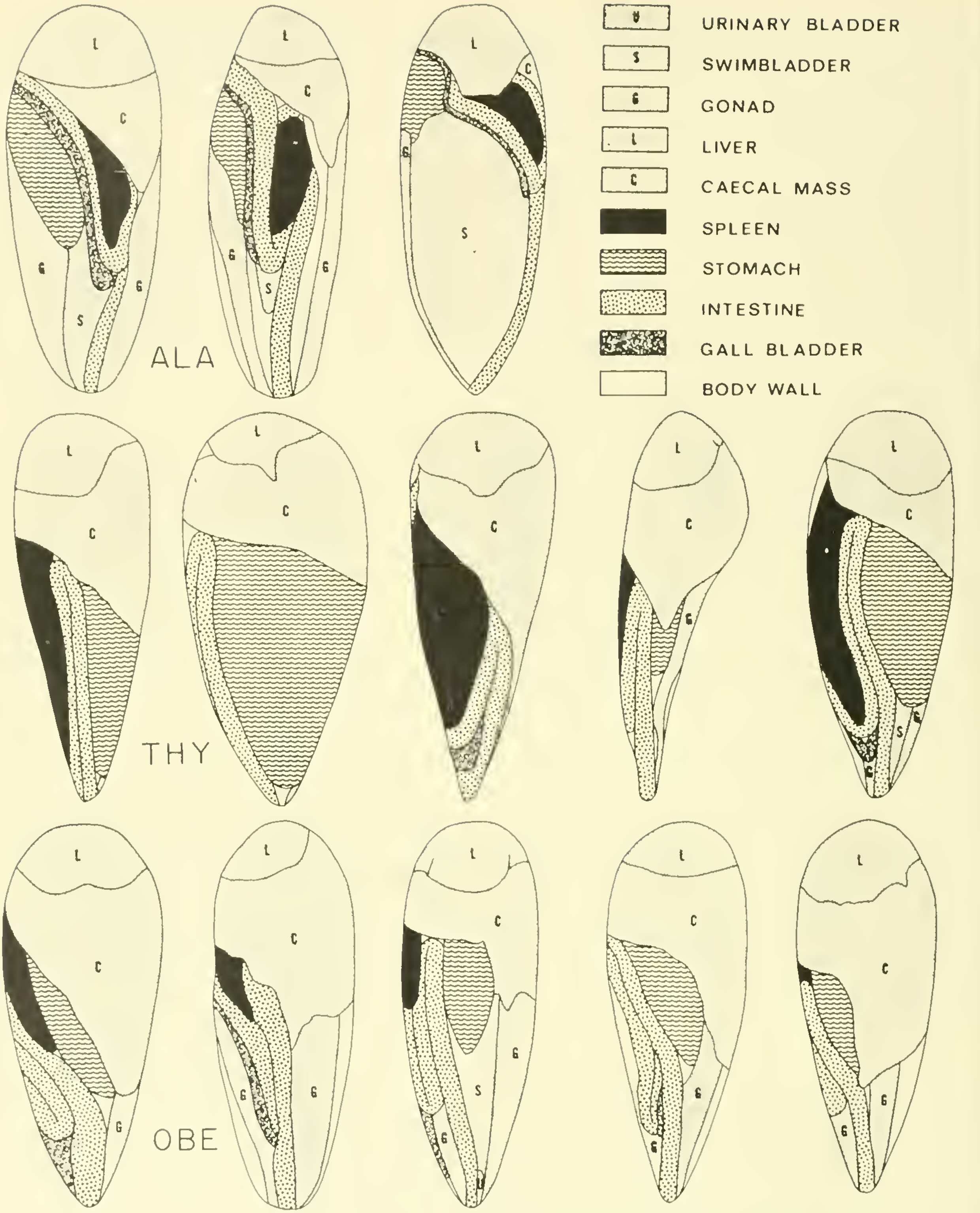


FIGURE 14.—Left lateral view of vertebrae 35–39, showing differences in proportions of vertebra 36. (top) *Thunnus albacares,* (middle) *T. alalunga,* (bottom) *T. obesus,* typical of other species not illustrated.

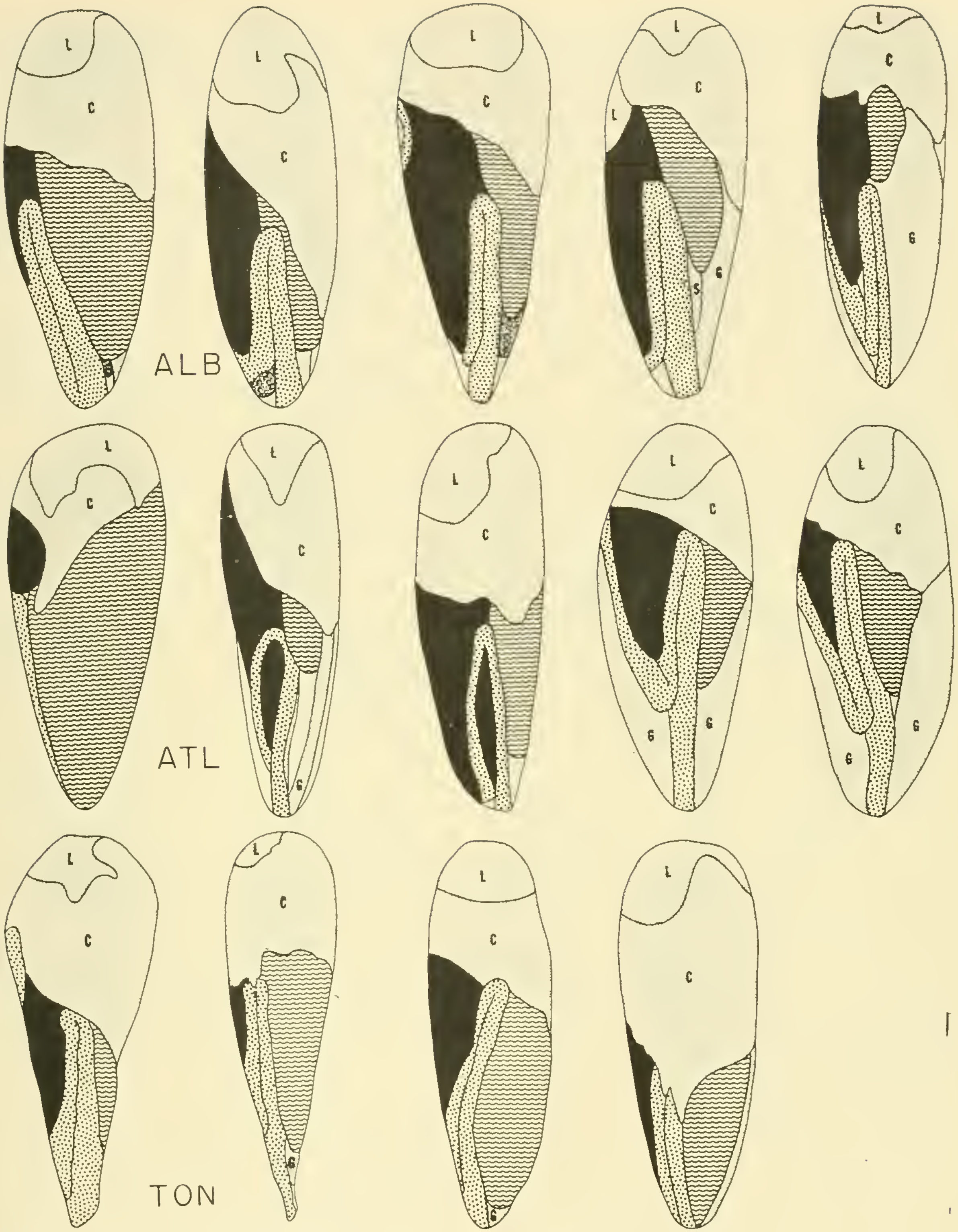
Digestive System and Associated Organs

General Description.—At the anterior end of the body cavity the liver abuts against the transverse septum and caps the other organs. It is usually composed of three lobes, only the middle of which is plainly visible in ventral view; the other two lobes lie along the lateral body wall, hidden by the other organs. The ventral surface of the liver of some species appears striated owing to the parallel arrangement of blood vessels (both arterial and venous) near its surface. The species with striated livers also possess, on the dorsal surface of the liver, several large "vascular cones," each comprising numerous vessels bound in a common sheath. These are absent in species with unstriated livers. In all species (Morice, 1953, to the contrary) there are two efferent (venous) vessels leading directly from the anterior surface of the liver into the sinus venosus. The esophagus merges indistinguishably (in external view) into the stomach, which forms a blind sac posteriorly. The intestine rises from the anterior



U URINARY BLADDER
S SWIMBLADDER
G GONAD
L LIVER
C CAECAL MASS
SPLEEN
STOMACH
INTESTINE
GALL BLADDER
BODY WALL
ALA
THY
OBE

FIGURE 15.—Ventral view of in situ visceral patterns of *Thunnus* species. Arranged from left to right in order of increasing fork length. ALA—780, 875, 1,030 mm.; ALB—637, 700, 808, 1,340,



1,420 mm.; ATL—337, 438, 513, 563, 650 mm.; OBE—1,250, 1,310, 13,50 1,450, 1,540 mm.; THY—457, 750, 872, 1,050, 1,670 mm.; TON—373, 392, 910, 924 mm.

end of the stomach, and a very large caecal mass is attached to its origin by several ducts that are not externally apparent. The intestine proceeds caudad for half or more the length of the body cavity (straight intestine), forms a loop, runs craniad (ascending portion) almost to the pylorus, then forms another loop and continues in a nearly straight line (descending portion) to the anus. The spleen is located between the straight and ascending portions. The gall bladder is a long, tubular sac rising from the right lobe of the liver, attached to the dorsal wall or the left side of the straight intestine. A swimbladder, when present, is situated dorsad to the main visceral mass, and may be rudimentary or well developed.

Specific Characters.—The ventral surface of the liver (fig. 16) is striated in *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus.* These striations give the impression of being denser and extending farther toward the center of the middle lobe in *T. alalunga*, *T. maccoyii*, and *T. thynnus* than in *T. obesus*, but this difference is not easy to detect. We have seen only one instance of striations being limited to the peripheral margins, at least of the middle lobe, as described by Kishinouye (1923) and Godsil and Byers (1944) for Pacific, and by Morice (1953) for Atlantic *T. obesus.* The peripheral nature of these striations has been used as a major diagnostic character of the nominal genus *Parathunnus.* In *T. albacares*, *T. atlanticus*, and *T. tonggol* the liver lacks striations.

In *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus* the three liver lobes are subequal in length, the lateral lobes most often slightly shorter than the middle lobe. In *T. albacares*, *T. atlanticus*, and *T. tonggol* the right lobe is much longer and narrower than the middle or left lobe.

Correlated with the ventral striations on the livers of *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus*, vascular cones are associated dorsally with each lobe. The middle lobe always has a single large cone; the other lobes usually have two or more, and these may be somewhat difficult to distinguish from ordinary blood vessels. In the left lobe, we recorded two to five cones in *T. alalunga;* two to six, usually two or three, in *T. thynnus;* two to four in *T. maccoyii;* one to six, usually one or two, in *T. obesus.* In the right lobe we found: two to eight, usually two, in *T. alalunga;* one or two, usually two, in *T. thynnus;* two in *T. maccoyii;* one to four, usually one or two, in *T. obesus.*

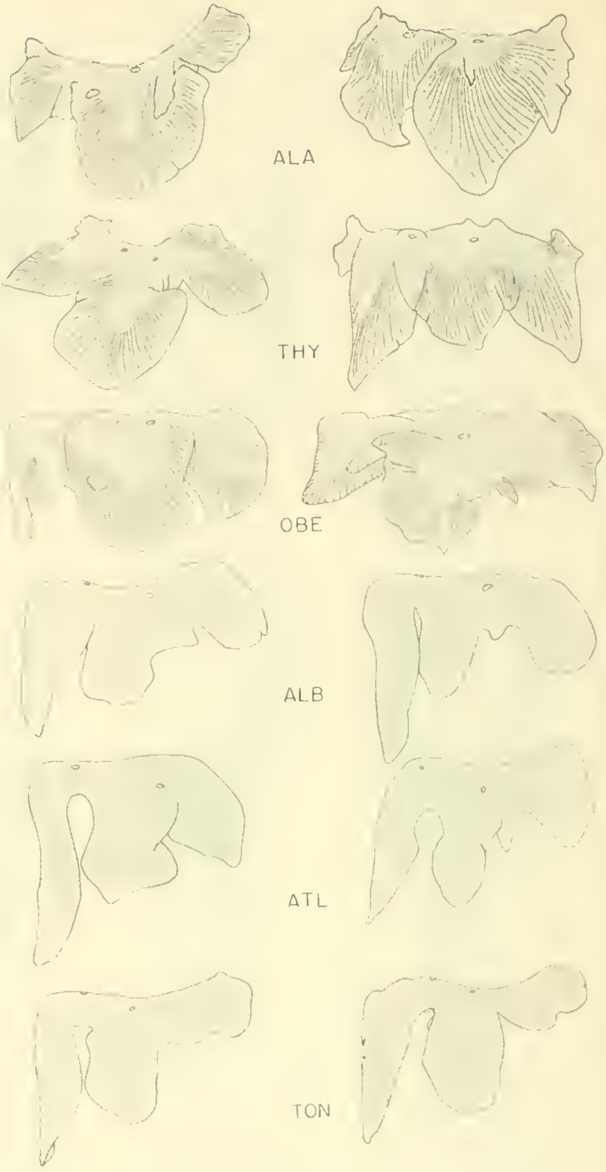


FIGURE 16.—Ventral view of livers of *Thunnus* species, showing shape and presence or absence of striations. Fork lengths (left, right): ALA—875, 1,030 mm.; ALB—700, 1,175 mm.; ATL—568, 650 mm.; OBE—1,450, 1,540 mm.; THY—457, 757 mm.; and TON—910, 924 mm.

Morice (1953) described the liver of *T. albacares* as having two efferent vessels at the anterior end, but noted only a single vessel in *T. alalunga*, *T. thynnus*, and *T. obesus.* He probably overlooked the vessel in the right lobe near the junction with the middle lobe, because this vessel is smaller than the one in the middle lobe. All specimens that we examined had two such efferent vessels.

Thunnus alalunga has the spleen on the left side and the stomach on the right. In the other species these positions are reversed (fig. 15).

Godsil and Byers (1944) attached considerable importance to their observation that the straight intestine in *T. alalunga* crosses from the right to the left side, and the descending portion lies on the left side. This course is obviously correlated with the position of the stomach in this species. We found that the intestine often does not cross over so obviously and that the descending portion is commonly near the middle. Thus there is little or no difference between *T. alalunga* and the other species in position of the descending intestine, although the side on which the intestine originates is different.

The relative position of the first loop of the intestine (where the straight intestine forms the ascending portion) differs to a degree among the species (fig. 15). In *T. alalunga* this loop is shortest and is located about one-half to two-thirds the distance between the posterior margin of the middle liver lobe and the anus. In the other six species the loop may reach from about three-fourths to nine-tenths of the liver-anus distance. In Pacific forms, *T. alalunga* is reported by Godsil and Byers (1944) to have a short "fold" (27–41 percent of body cavity), *T. albacares* a slightly longer "fold" (36-61 percent), and *T. thynnus orientalis* and *T. obesus* a long "fold." Their illustrations and measurements, and our observations, indicate such a wide range of variation that only *T. alalunga* can be regarded as distinct in this character.

One Atlantic specimen of *T. obesus* among our study material had two intestinal loops, a situation never before reported to our knowledge.

The length of the spleen (fig. 15) is normally short, seldom reaching beyond half the distance from caecal mass to end of body cavity in *T. alalunga*, *T. obesus*, and *T. atlanticus*, but usually long, reaching at least three-fourths of this distance in *T. thynnus*, *T. maccoyii*, and *T. albacares; T. tonggol* is variable. In all species there are exceptions.

The gall bladder (fig. 15) in *T. alalunga* is normally exposed along the entire right side of the straight intestine. In the other species it is usually either entirely hidden or a small portion may appear posterior to the first intestinal loop; in the few specimens in which it was largely exposed, the visceral mass seemed to be distorted.

The swimbladder (fig. 17) appears to be invariable and distinctive only in *T. obesus*, in which it is long, usually slender, beginning near the transverse septum, and tapering to a point that reaches the posterior end of the body cavity.

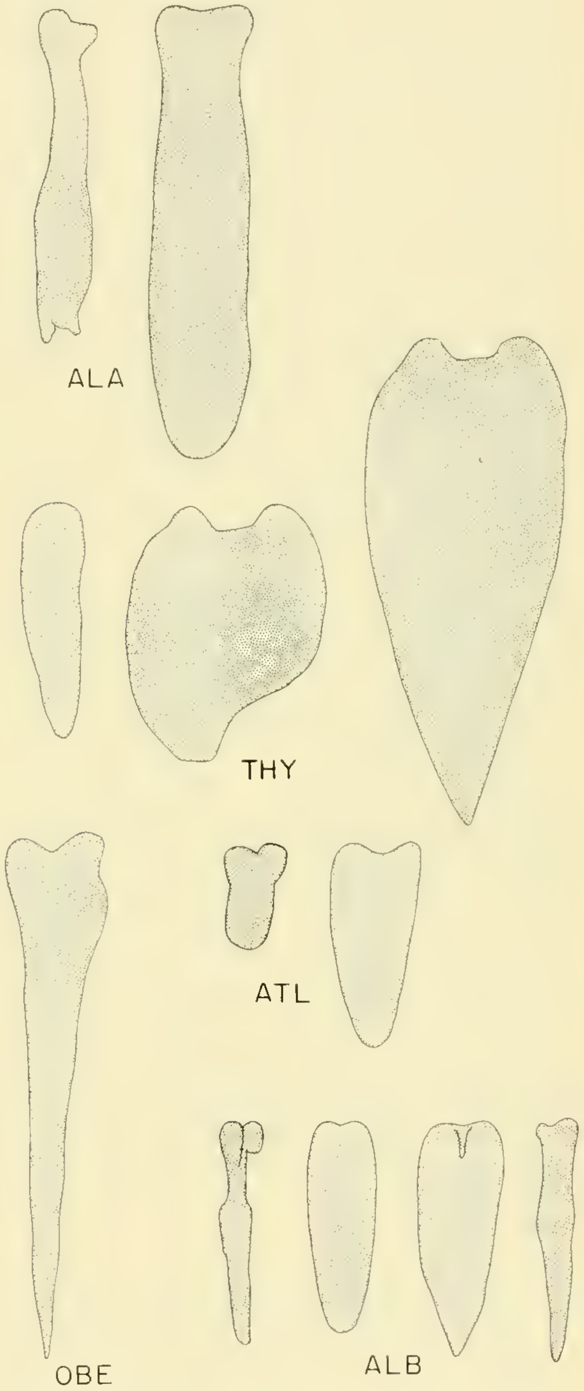


FIGURE 17.—Ventral view of swimbladder shapes of *Thunnus* species. Fork lengths (left to right): ALA—875, 1,030 mm.; ALB—637, 700, 1,175, 1,420 mm.; ATL—650, 664 mm.; OBE—1,250 mm.; and THY—954, 1,050, 1,670 mm.

Absence of a functional swimbladder in *T. tonggol* may be regarded as a useful diagnostic character, but in most specimens we discovered a tiny swimbladder, about 4 mm. in diameter, which could easily have been overlooked. A very small swimbladder (ca. 20 mm. long) also was present in two *T. maccoyii* (742 and 764 mm.).

Variation in the other five species is considerable (fig. 17). In *T. atlanticus* the swimbladder may be short, oblate, lying far anterior in the body cavity; or it may approach the length of a poorly developed swimbladder of *T. albacares*. In the latter case, the swimbladder is comprised of two chambers divided by a transverse membrane, with the anterior chamber probably representing the small type of swimbladder, the posterior chamber an addition. In *T. albacares* the swimbladder is moderately long, usually reaching about the level of the 14th or 15 vertebra (range 12–17). In *T. alalunga* it varies from narrow, only moderately long, and deflated, to fully the length of the body cavity and inflated to fill much of the cavity.

In *T. thynnus* and *T. maccoyii* variation in swimbladder dimensions may be correlated with growth. The changes in swimbladder dimensions were recognized by Serventy (1956a: 10), and were suggested but not recognized by Godsil and Holmberg (1950: 21). Smaller specimens (457–954 mm.) have rudimentary swimbladders that are slender, deflated, and short (about 6 vertebrae long), about a quarter of the length of the body cavity, and do not reach the depression anterior to the dorsal bulge. In two *T. maccoyii* the swimbladder was tiny and could easily have been missed in a casual dissection. In a 1,060-mm. specimen of *T. t. thynnus* the organ was inflated and occupied about half the body cavity (fig. 17). In specimens 1,390-mm. and larger the swimbladder extends from the depression anterior to the kidney almost or quite to the posterior end of the body cavity; it is as wide as the body cavity in its anterior half and posteriorly tapers almost to a point.

Urogenital System

General Description.—The paired gonads are frequently visible in ventral view. They lie along the dorsolateral body wall, their posterior ends forming ducts which open on each side of the urinary papilla. The kidney is anterior in position and dorsal to the layer of fibrous connective tissue overlying the swimbladder. Its anterior margin usually follows the edges of the depression anterior to the hump formed by the haemal arches, and lateral extensions reach forward in a semicircle and sometimes nearly meet anteriorly. Depending upon the species, a posterior extension ("tail") may reach about as far as the level of the 16th vertebra; and *T. albacares* sometimes has accessory masses of kidney tissue posterior to the main mass. In the anterolateral extensions of the kidney, the urinary ducts ("ureters") arise and join within or just posterior to the kidney substance, and the resulting single duct proceeds posteriorly. Just before the anus, the duct enters a small but prominent urinary bladder, which may lie within the mesenteries of the gonads or project freely into the body cavity, depending upon the species. The urinary bladder empties through a urinary papilla behind the anus.

Specific Characters (fig. 18). The kidney of *T. alalunga* is unique in lacking a "tail," the end reaching the level of the 7th to 9th vertebra (11th in one specimen). In *T. thynnus* and *T. maccoyii* the tail is relatively short, reaching the 8th to 11th vertebra. Its configuration varies in Atlantic specimens from tapering to truncate, encompassing all the forms used by Godsil and Holmberg (1950) to differentiate *T. maccoyii* from Atlantic and Pacific *T. thynnus*. None of our *T. maccoyii* had truncate kidneys. In *T. obesus* the tail is slightly longer than in *T. thynnus*, reaching the 11th to 14th vertebra, is narrower, and is more distinctly delimited from the anterior kidney mass. The kidney of *T. albacares* has a long tail, tapering gradually from the anterior kidney mass and reaching the 12th to 16th vertebra; accessory kidney masses are often present posteriorly. In *T. atlanticus* the kidney mass is bulky anteriorly and has a long, narrow tail that reaches the 12th to 17th vertebra. In *T. tonggol* there is a large anterior portion and a long, narrow tail that reaches the 15th to 17th vertebra.

The branching of the ureters varies considerably, but shows some general tendencies that, together with the shape of the kidney, are useful in distinguishing species (fig. 18). In the tailless kidney of *T. alalunga*, the two main branches are widely divergent, joining at the posteriormost end of the kidney substance. In *T. thynnus* and *T. maccoyii* the junction may occur at the posterior end, at some distance craniad, or just posterior to the kidney. The angle formed by the branches is small when the junction is well posterior, large when far anterior. In *T. obesus* the branches converge to run close together and almost parallel for a considerable dis-

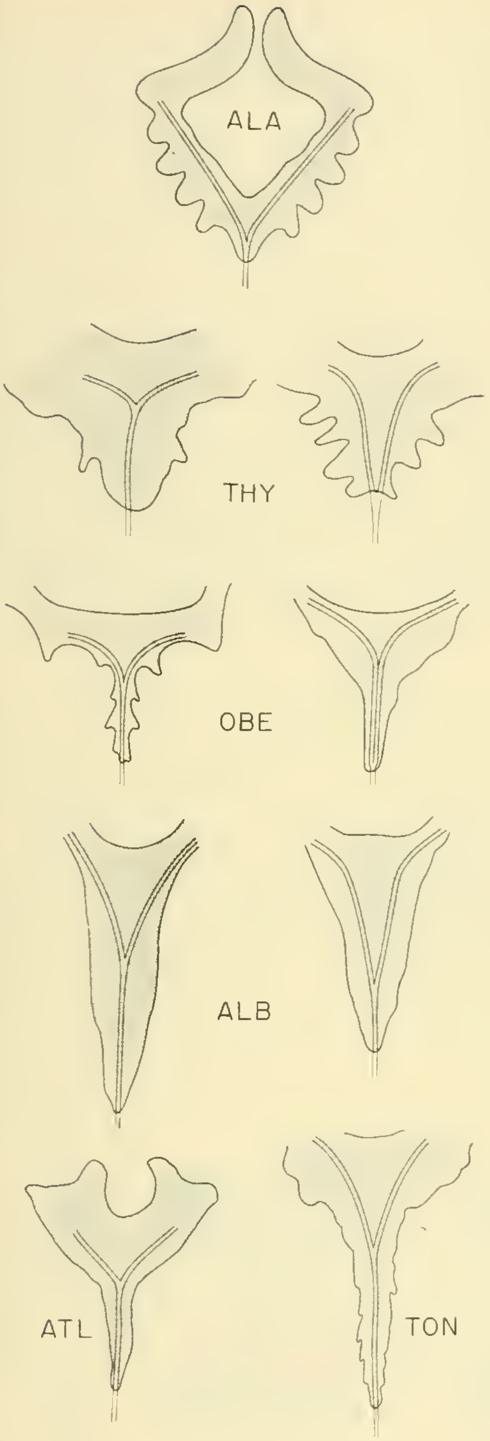


FIGURE 18.—Ventral view of kidney and ureter of *Thunnus* species. Forward extent shown only in ALA and ATL. Fork lengths (left, right): ALA—875 mm.; ALB—700, 1,175 mm.; ATL—533 mm.; OBE—1,310, 1,350 mm.; THY—457, 872 mm.; and TON—910 mm.

tance before they join at the posterior end of the kidney. In those specimens in which the junction occurs well forward, the angle between the branches is less than in *T. thynnus* or *T. maccoyii*. In *T. albacares* and *T. tonggol* the branches usually converge gradually, at a very slight angle, and join at some distance craniad from the end of the kidney tail. When the junction is almost at the posterior end of the tail, the branches may be almost parallel for a short distance. The junction of the branches in *T. atlanticus* usually occurs far anteriorly, and the angle between the branches is usually large. Some specimens, however, resemble *T. albacares*.

Our observations on the urinary bladder are few, but they suggest more variation than was implied by Godsil and Byers (1944). The extent to which the bladder is embedded in the dorsal body wall or projects freely into the body cavity seems to be partly a matter of interpretation. In all species, most of the bladder was contained in the membrane between the left and right gonads. Some *T. thynnus* and *T. alalunga* had much of the posterior part closely attached to the body wall, but the anterior part was separated from the body wall and contained in the membrane of the gonads. The anterior tip of the bladder actually projected free of the membrane in some specimens of *T. obesus*. In all three of these species, at least some specimens had the bladder, except for its posteriormost end, entirely within the membrane, not attached to the body wall, and without a freely projecting anterior tip; this was the only condition observed in the other four species.

Dorsal Connective Tissue

Covering most of the dorsal body wall, dorsal to the peritoneum but ventral to the kidney, is a region of tough, white fibrous connective tissue. In *T. alalunga* the sheet becomes extremely thick posteriorly. In *T. albacares* a thick raised median cord forms in the anterior half. The other species have a rather uniform thin sheet of tissue, perhaps slightly thickened posteriorly.

VASCULAR SYSTEM

Important papers on the circulatory system of *Thunnus* include those of Kishinouye (1923), Godsil and Byers (1944), and Godsil and Holmberg (1950).

General Description

The pericardial cavity is separated from the pleuroperitoneal cavity by a transverse septum, the walls of which are formed posteriorly by peritoneum, anteriorly by pericardium and the walls of the sinus venosus and the ducts of Cuvier, which enter the sinus. No specific differences have been observed in these structures or in the heart itself.

After leaving the heart, blood is carried in the ventral aorta, which sends an afferent branchial artery into each of the gill arches. After circulating in the capillaries of the gill lamellae, the blood from each gill arch enters an efferent branchial (epibranchial) artery. The anterior two epibranchials of each side unite to form a common trunk, and these trunks join as the "Y" of the aorta, usually beneath the second vertebra, to form the dorsal aorta (fig. 19). The posterior two epibranchials of each side also unite, and their short common trunks join the dorsal aorta, usually beneath the third vertebra. The dorsal aorta continues posteriorly along the dorsal body wall to the first haemal canal. The coeliaco-

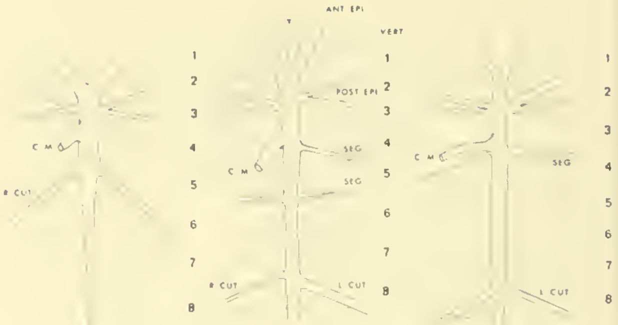


FIGURE 19.—Representative patterns of anterior branches of dorsal aorta in *Thunnus* species. (Left) *T. alalunga;* (middle) *T. atlanticus;* (right) *T. tonggol.* Y: Y of aorta. ANT EPI: anterior epibranchials. POST EPI: posterior epibranchials. C–M: coeliaco-mesenteric. SEG: segmental. L. CUT and R. CUT: Left and right cutaneous. VERT: vertebrae separated by dashed lines.

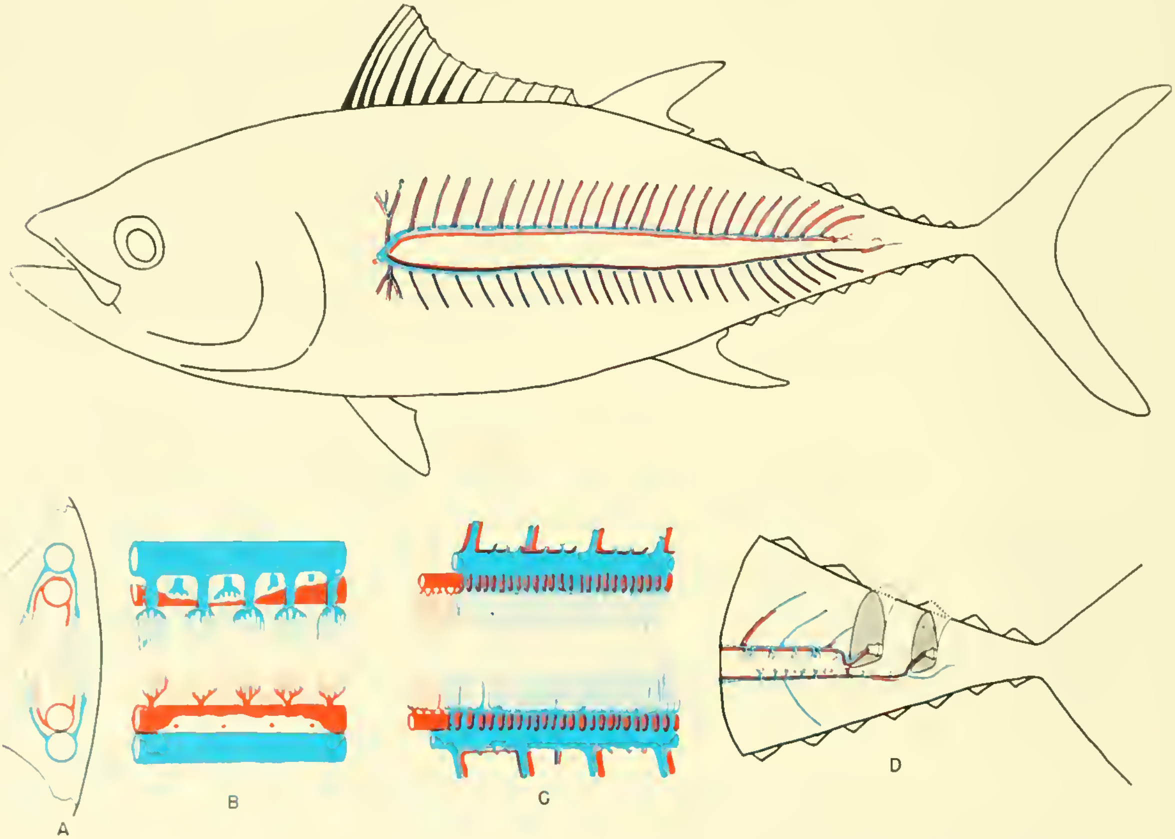


FIGURE 20.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus obesus.* (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, with portions of the arterial walls cut away to show origin of arterioles and venules. (C) Enlarged lateral view of cutaneous vessels. (D) Posterior course of cutaneous vessels; no posterior commissure. From Godsil and Byers, 1944 (fig. 66).

mesenteric artery arises from the dorsal aorta beneath the third to fourth vertebra and forms two or three main branches that go to the liver, supply the vascular cones when present, and give off branches to the other visceral organs. The paired cutaneous arteries rise posterior to the origin of the coeliaco-mesenteric artery and course laterad almost or quite perpendicular to the aorta; they penetrate the lateral body musculature, and on each side form two branches beneath the skin that almost parallel one another to the caudal peduncle (fig. 20, 21). At about the level of the 30th vertebra, a posterior commissure may connect the dorsal and ventral branches of each side. Along their length, the lateral branches give off into their interspace arterioles, which are so dense that they seem to form a solid sheet penetrating the dark muscle (chiai).

Cutaneous veins accompany the arteries; the two parallel lateral branches join anteriorly on each side (fig. 22) to form a large vein that enters the duct of Cuvier, which in turn enters the sinus venosus.

If a post-cardinal vein is present it emerges from the first closed haemal arch, runs toward the right side in the kidney mass, and joins the right cutaneous vein. There is usually a cross-connection between the post-cardinal and left cutaneous veins.

Specific Characters

The coeliaco-mesenteric artery usually has two branches in *T. thynnus*, *T. maccoyii*, *T. alalunga*, and *T. atlanticus*, and three branches in *T. albacares* and *T. tonggol*. In *T. obesus* either two or three branches may be present in both Atlantic and Pacific specimens. Exceptions were noted in *T. albacares* and *T. atlanticus*.

A connecting branch near the liver between two of the coeliaco-mesenteric branches is present in *T. maccoyii*, may be present or absent in *T. thynnus*,

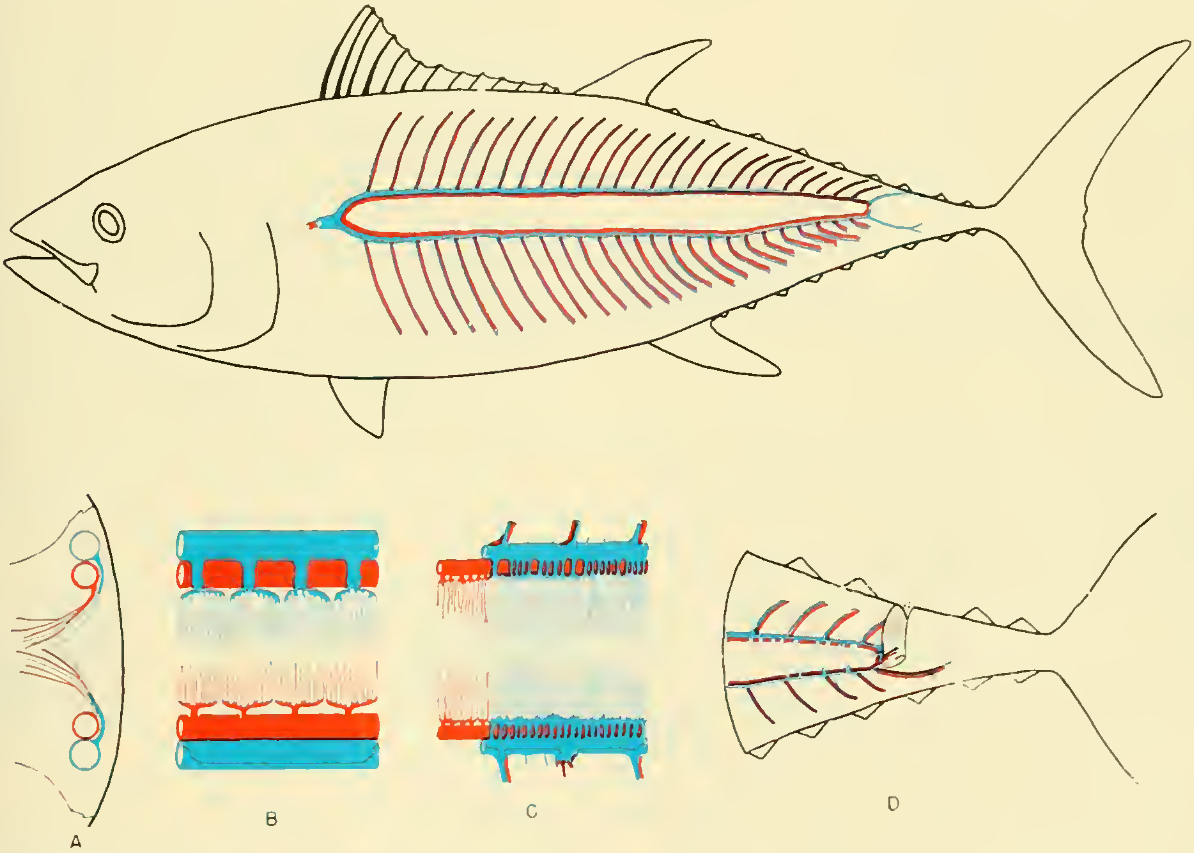


FIGURE 21.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus albacares*. (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, to show origin of venules (dorsal) and arterioles (ventral). (C) Enlarged lateral view of cutaneous vessels. (D) Posterior commissure. From Godsil and Byers, 1944 (fig. 31).

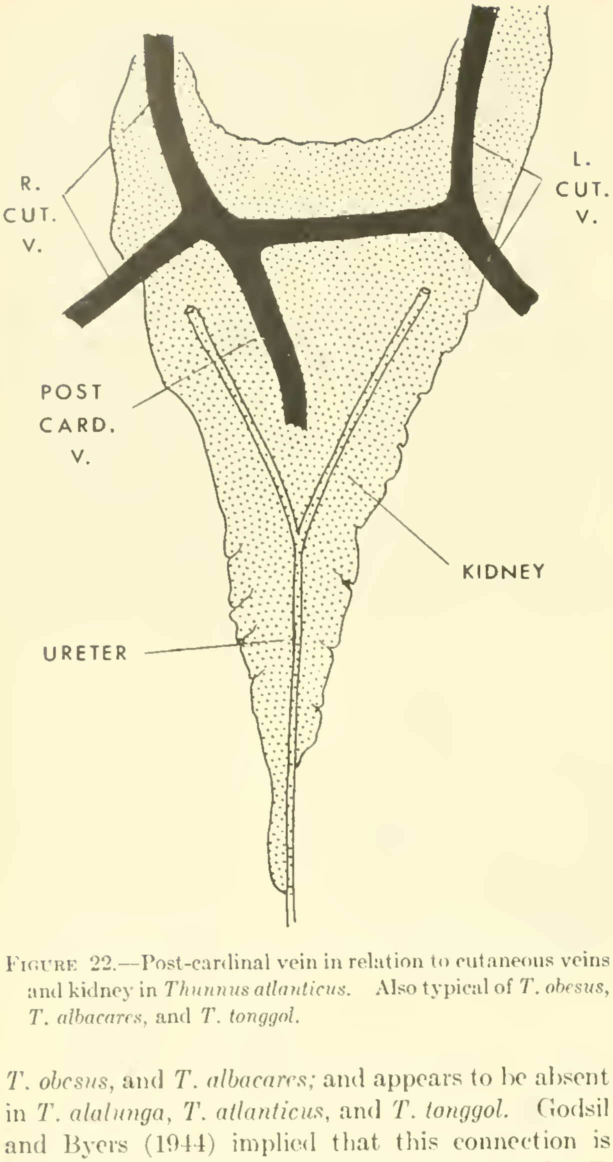


FIGURE 22.—Post-cardinal vein in relation to cutaneous veins and kidney in *Thunnus atlanticus*. Also typical of *T. obesus*, *T. albacares*, and *T. tonggol*.

T. obesus, and *T. albacares;* and appears to be absent in *T. alalunga*, *T. atlanticus*, and *T. tonggol*. Godsil and Byers (1944) implied that this connection is always, or nearly always, present in Pacific *T. albacares*. Godsil and Holmberg (1950) used its supposed absence in Atlantic *T. t. thynnus* as one character that differentiates Atlantic from Pacific specimens (*T. t. orientalis*), a conclusion which our observations do not support.

The cutaneous artery usually originates at the level of the third or fourth vertebra in *T. thynnus*, *T. maccoyii*, and *T. alalunga*, and at the sixth to eighth vertebra in *T. albacares*, *T. obesus*, *T. atlanticus*, and *T. tonggol*.

The cutaneous arteries pass laterally between the third and fourth ribs in all *T. thynnus*, *T. maccoyii*, and *T. alalunga* examined by us (also between the second and third according to Godsil and Holmberg, 1950); in *T. albacares*, *T. obesus*, *T. tonggol*, and *T. atlanticus* they pass between the fifth and sixth ribs, or occasionally between the fourth and fifth. Branching occurs between the fourth and fifth intermuscular bones in *T. thynnus*, *T. maccoyii*, and *T. alalunga*, and between the sixth and seventh in *T. albacares*, *T. obesus*, *T. tonggol*, and *T. atlanticus*. Godsil and Holmberg (1950) reported more *T. maccoyii* with branching between the fifth and sixth, and we observed this in one specimen of *T. t. thynnus*. In a significant number of our *T. albacares*, as well as two *T. obesus*, branching occurred between the seventh and eighth intermuscular bones.

A posterior commissure is present in *T. thynnus*, *T. maccoyii*, *T. albacares* (fig. 21), *T. tonggol*, and *T. atlanticus*, but absent in *T. alalunga*. In *T. obesus* it is present or absent (fig. 20). In all species except *T. albacares* and *T. maccoyii*, we encountered specimens in which we could not ascertain the presence of a commissure.

We noted the number and position of the rows of arterioles and venules arising from the lateral cutaneous vessels in relatively few specimens of each species (see fig. 23). *T. alalunga*, *T. albacares* (fig. 21), *T. atlanticus*, and *T. tonggol*, have one row from each vessel; in *T. alalunga* it originates on the mesial side, and in the other species on the lateral side. In *T. thynnus*, *T. maccoyii*, and *T. obesus* (fig. 20) two rows, one mesial and one lateral, arise from each vessel. Kishinouye (1923) reported two rows of venules and a single row of arterioles in Japanese *T. thynnus orientalis*. California specimens have two rows of arterioles (Godsil and Byers, 1944, and our observations). We feel certain that Kishinouye either was mistaken or relied on an unusual specimen.

In *T. albacares* large parallel trunks connect the posterior epibranchial and the cutaneous arteries on

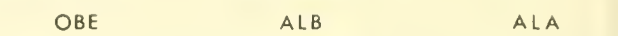


FIGURE 23.—Relationships of arterioles and venules to cutaneous artery (light) and vein (dark). Three patterns represented by *T. obesus* (OBE), *T. albacares* (ALB), and *T. alalunga* (ALA). Lateral view. After Kishinouye (1923).

each side; they are absent in the other species.

A post-cardinal vein joins the right cutaneous vein in *T. albacares, T. obesus, T. atlanticus,* and *T. tonggol;* it is absent in *T. thynnus, T. maccoyii,* and *T. alalunga.*

OLFACTORY ORGAN

As this manuscript was being completed, Iwai and Nakamura (1964b) described their use of the olfactory rosette to distinguish species of *Thunnus.* In each nasal cavity beneath the anterior naris is an olfactory rosette, consisting of numerous laminae arranged radially around a central axis. According to Iwai and Nakamura, *T. alalunga* is unique in having a pair of fleshy labia surrounding the short laminae. The laminae in *T. obesus* are described as smooth, greatly expanded distally with adipose tissue, and often partly fused distally. In *T. thynnus* the laminae in small specimens are smooth and of uniform thickness to the distal edge, whereas in larger specimens the laminae are smooth and distally expanded, but with little evident adipose tissue. *Thunnus maccoyii* is differentiated from *T. thynnus* by the presence, in some specimens, of slight fringing in the distal ends of the laminae. In *T. albacares* and *T. tonggol* the laminae are entirely fringed on their distal edges; and in large *T. albacares* the basal half of the rosette is densely spotted with pigment; however, Iwai and Nakamura admit that the rosettes of *T. tonggol* and small *T. albacares* resemble each other, and, from their figure 3, also resemble those of *T. maccoyii.* On the basis of admittedly insufficient material, Iwai, Nakamura, and Matsubara (1965) indicate that the nasal rosettes of *T. atlanticus* closely resemble those of *T. tonggol* except that the laminae of the former tend to have the distal ends folded inward.

We have examined very few nasal rosettes, but our observations indicate a need for more careful scrutiny of this character, with respect to normal variation and growth changes, before it is used widely. A specimen of *T. alalunga* and two of *T. obesus* agreed with Iwai and Nakamura (1964b), but in one *T. obesus* the laminae were lightly pigmented and had short, flat fimbriae along their entire length. Two specimens of *T. albacares* were distinctive in the abundance of pigment in the laminae, but while in one the fimbriae were very pronounced and fingerlike, in the other they were less developed and flatter. Rosettes of one *T. atlanticus* and one *T. tonggol* were virtually identical and were similar to those of *T. albacares,* with dense, short, flat fimbriae on the laminae, but had less abundant pigment; folding of the distal ends of the laminae was not apparent in either species. In a larger specimen of *T. thynnus* from Cape Town, South Africa, the laminae were almost uniform in thickness to the distal edge and bore prominent flattened fimbriations along most of their length. These observations are enough at variance with those of Iwai and Nakamura that they clearly show the need for further study.

MERISTIC CHARACTERS

The species of *Thunnus* are essentially identical in the number of fin rays (table 1). The number of gill rakers is the only meristic character that we have found valuable in separating species of *Thunnus* (table 2).

Species Differences.—*T. atlanticus* has fewer gill rakers (19–25) than any other species of *Thunnus* in the Atlantic, and *T. tonggol* has fewer (19–26, rarely to 28) than any other *Thunnus* in the Indo-Pacific (table 2). *T. thynnus* and *T. maccoyii* have the greatest number of gill rakers in the genus (31–43). The other three species fall between these two groups with a combined range 23–35. The overlap between species with low, medium, and high numbers of gill rakers is very slight. The *T. thynnus-maccoyii* complex shows differences of some magni-

TABLE 1.—Range of variation in fin-ray counts in the species of *Thunnus*

[Based on original and published data]

Fin	Species					
	T. alalunga	*T. albacares*	*T. atlanticus*	*T. obesus*	*T. thynnus*	*T. tonggol*
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Dorsal spines	12–14	12–14	12–14	13–14	12–14	11–14
Second dorsal rays	13–16	13–16	12–15	14–16	13–15	14
Dorsal finlets	7–9	8–10	7–9	8–10	8–10	9
Total second dorsal rays	21–24	22–24	20–23	22–24	22–24	23
Anal rays	13–15	12–15	11–15	11–15	13–16	14
Anal finlets	7–9	7–10	6–8	7–10	7–9	8
Total anal rays	20–23	21–23	19–22	21–23	21–24	21–23
Pectoral rays	31–36	33–36	31–35	31–35	30–36	30–35

TABLE 2.—Total number of gill rakers on the first arch in the species of *Thunnus*

Number of rakers	*T. tonggol*			*T. atlanticus*	*T. obesus*			
	West Indian-Red Sea	SE Asia	Australia	West Atlantic	West Atlantic	East Atlantic	Central-West Pacific	East Pacific
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
19			3	1				
20		2	18	7				
21	1	2	43	29				
22		2	86	59				
23	4	4	54	21			1	
24	1	2	19	2			5	1
25	3		2	1	5	1	27	3
26	10				13	4	159	26
27	1				15	6	147	28
28	1				17	3	70	17
29					4	4	23	12
30						1	14	
31						1	2	
Number of fish	21	12	225	120	55	20	448	87
Average	25.1	21.7	22.0	21.9	27.3	27.6	26.9	27.1
Sources	6, 15, 17	6	6, 13, 25	2, 6, 12, 17	6, 12	6	3, 5, 30	5, 6, 8, 30

	T. alalunga					*T. albacares*				
	West Atlantic	East Atlantic	Indian Ocean	Central-West Pacific	East Pacific	West Atlantic	East Atlantic	West Indian Ocean	Central-West Pacific	East Pacific
25	1								1	
26	1	4	1	6	1		2	2	3	
27	10	18	5	45	6	6	3	7	24	2
28	20	55	9	142	21	11	11	22	73	8
29	15	50	15	176	26	33	51	54	194	20
30	6	27	11	96	8	37	88	58	212	50
31	2	4	1	15	2	30	126	23	202	51
32				1		9	80	5	93	24
33						1	23		21	6
34							7		2	
35							1			
Number of fish	55	158	42	481	64	127	392	171	855	161
Average	28.3	28.6	28.8	28.8	28.6	29.8	30.8	29.5	30.0	30.5
Sources	6, 12	6, 10, 11	14, 28, 29	5, 8, 29, 30	5, 8, 30	6, 12, 17	6, 11, 23	6, 19, 28	5, 8, 21, 22, 30	5, 8, 20, 30

	T. maccoyii		*T. t. orientalis*		*T. t. thynnus*	
	South Africa	Australia	Central-West Pacific	East Pacific	West Atlantic	East Atlantic-South Africa
31	1	10				
32	2	62		2		
33	3	84		2		
34	5	89		2	3	
35	1	54	3	14	2	4
36	1	25	6	10	12	8
37		6	2	11	32	40
38			1	2	63	88
39				2	102	105
40		1	1		40	74
41					29	36
42					4	7
43					1	4
Number of fish	13	331	13	45	288	366
Average	33.5	33.7	36.4	35.8	38.8	38.9
Sources	26	1, 5, 6, 9, 24	5, 6	6, 9, 12	6, 7, 9, 12	6, 18, 26, 27

Source:
1—Abe, 1955; 2—Beebe and Tee-Van, 1936; 3—Brock, 1949; 4—Crane, 1936; 5—Dung and Royce, 1953; 6—Gibbs and Collette, original data; 7—Ginsburg, 1953; 8—Godsil and Byers, 1944; 9—Godsil and Holmberg, 1950; 10—Letaconnoux, 1951; 11—Marchal, 1959; 12—Mather, 1964; 13—Munro, 1957; 14—Postel et al., 1960; 15—Ranade, 1961; 16—Rivas, 1954b; 17—Rivas, 1961; 18—Robins, 1957; 19—Royce, 1965; 20—Schaefer, 1948; 21—Schaefer, 1952; 22—Schaefer, 1955; 23—Schaefer and Walford, 1950; 24—Serventy, 1956a; 25—Serventy, 1956b; 26—Talbot, 1964; 27—Tiews, 1963; 28—Williams, 1964; 29—Yoshida and Otsu, 1963; 30—Japan Fishery Agency, 1964.

tude among populations in both the means (Atlantic 38.9, Pacific 35.9, *T. maccoyii* 33.7) and the modes (39, 35, 34). These differences and others can be used to separate the two subspecies, *T. thynnus thynnus* in the Atlantic and *T. thynnus orientalis* in the Pacific, and *T. maccoyii* in the southern Pacific and Indian oceans. Populations of *T. tonggol* in the Red Sea and western Indian Ocean appear to have more gill rakers than those to the eastward.

MORPHOMETRIC CHARACTERS

Relative lengths of body parts have limited value in species identification of tunas, although they have been widely used by many investigators. Allometric growth has been demonstrated for many, if not most, body parts and has been responsible for many misconceptions. A classic example of allometry involves the dorsal and anal fins of *T. albacares* which become relatively much longer in large specimens. Furthermore, the length attained by these fins varies geographically in a complex fashion (Royce, 1965). Lack of consideration of these factors has resulted in the description of numerous nominal species. Many limited analyses have shown statistically significant differences between populations of widely distributed species (cf. Kurogane and Hiyama, 1957b, 1958a, 1959 for *T. alalunga*).

Of the many measurements that can be made, only the following appear to be of importance in distinguishing tuna species: dorsal and anal fin heights, pectoral fin length, placement of second dorsal fin, greatest body depth, and diameter of eye (or orbit).

Our conclusions are based, as often as possible, on data from many parts of the range of each species. Where these data have shown no noteworthy geographic differences, we consider them together as a single unit. Otherwise, the differences are mentioned. In addition to our original data, we have leaned heavily upon Dung and Royce (1953) for raw data, and have used many other sources. Our information has significant gaps that can be filled only by future work or by use of unpublished data from other workers. All species are more or less deficient in morphometric data for specimens below 400 mm. For the Atlantic, such data are few or lacking for *T. alalunga* less than 900 mm.; for *T. atlanticus* larger than 650 mm.; and for *T. obesus* less than 1,000 mm. For the Pacific and Indian Oceans, *T. maccoyii* is represented by data on only four specimens outside the 650–750 mm. range, and our sparse Indian Ocean data for all species are almost entirely from specimens sent to us as a result of cruises of the R/V *Anton Bruun* during the International Indian Ocean Expedition. Our interpretations must be judged with these deficiencies in mind.

Heights of the second dorsal and anal fins have received much attention, especially in *T. albacares*, in which the positive allometry of both these fins relative to fork length, apparently characteristic of all species, is most pronounced. This allometry has led to the description of long-finned nominal species in both the Atlantic and Pacific and even to the establishment of a new genus (*Semathunnus*). The species are compared in figs. 24 and 25, in which the large *T. albacares* are western Atlantic specimens. The few data for *T. maccoyii* fall in the range of *T. thynnus* and are not discussed separately.

As many workers have shown and as Royce (1965) has most recently demonstrated, different popula-

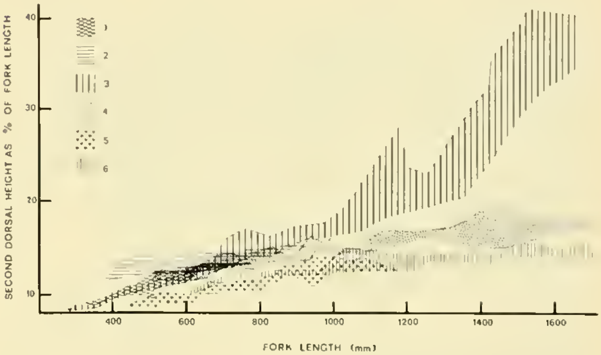


FIGURE 24.—Relative height of second dorsal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

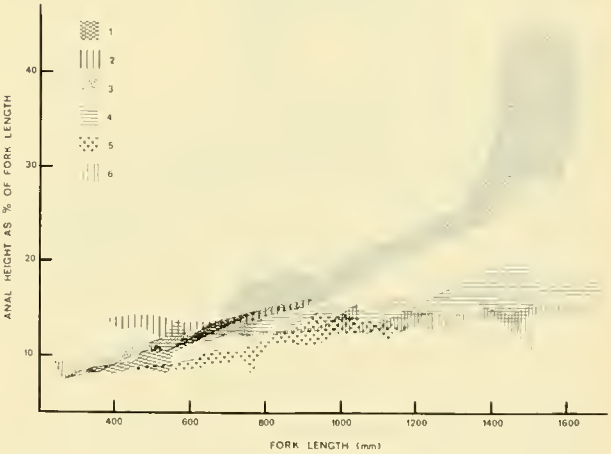


FIGURE 25.—Relative height of anal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

tions of *T. albacares* show different regressions, but in adults of this species the fins always become higher than in any other species of *Thunnus*. In the equatorial Pacific the fin heights vary in clinal fashion from highest in the west to lowest in the east. Western Atlantic specimens have very high fins, thereby resembling those from the western equatorial Pacific; eastern Atlantic (Angola) specimens have lower fins, as do those from the eastern Pacific.

At sizes between 350 and 600 mm., *T. tonggol* appears to have higher fins than any other species of *Thunnus*. From about 500 to 800 mm., *T. alalunga* has the lowest fins. The other five species are difficult to distinguish until about 700 mm. Beyond 800 mm., *T. albacares* clearly develops the highest fins, *T. thynnus* and *T. alalunga* remain the shortest, and *T. obesus* and *T. tonggol* are intermediate.

The pectoral fin shows a growth pattern that is probably similar in all species, but which differs among the species in size of fin and fork length at times of inflection. Simply stated, the pectoral fin undergoes a period or stanza of increase in length relative to fork length in juveniles, followed by an isometric period that leads into a final and continuous stanza of relative decrease in length (fig. 26). Size range of the stanzas is shown in table 3 for each adequately represented species. The smallest *T. tonggol* for which data were available are probably in the size range at which the distinction between increasing relative fin size and isometry is difficult to distinguish; hence the stanzas could not be determined.

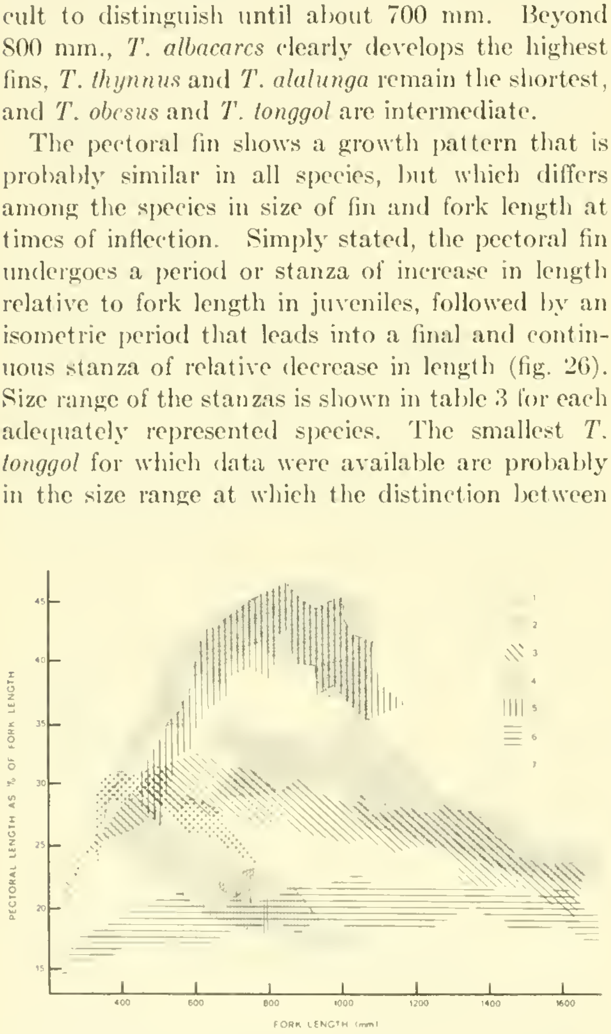


Figure 26.—Relative length of pectoral fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 12, 21, 27, 28, 42, 45–50), Godsil and Holmberg (1950: 54–55), and Serventy (1956b). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus;* 7—*T. maccoyii.*

Table 3.—*Approximate range in fork length of growth stanzas of pectoral fins in species of* Thunnus. *Smallest size limited by available data*

Species	Increase	Isometric	Decrease
	Millimeters	*Millimeters*	*Millimeters*
alalunga	450–700	700–900	900 +
obesus (Indo-Pacific)	350–700	700–900	900 +
obesus (Atlantic)	?	?650–1,000	1,000 +
albacares	250–500	500–650	650 +
atlanticus	? –350	350–500	500 +
tonggol	?	?	?400 +
thynnus	150–850	850–1,600	1,600 +
maccoyii	?	?650–1,450	?

At less than 500 mm., only *T. thynnus* is distinct, with pectorals 21 percent of fork length or less. Data for *T. maccoyii* are lacking. All other species overlap more or less in the 25–31 percent range, although between 400 and 500 mm. species distinctions begin to be apparent (viz. Pacific *T. obesus* pectorals become relatively longer, those of *T. tonggol* shorter).

The marked positively allometric growth of the pectorals of *T. alalunga* and Pacific *T. obesus* makes these two forms clearly distinctive from all others between 500 and 1,200 mm. (fig. 26). Most specimens have fins 34–46 percent of fork length. Up to 700 mm., *T. alalunga* has slightly shorter fins than Pacific *T. obesus*, but from 700–1,200 mm. they are virtually identical. Atlantic *T. obesus* in the 650–1,200 mm. range (no data were available for smaller specimens) appear to have significantly shorter pectorals than Pacific specimens: 29–35 percent at sizes of 650–1,000 mm., then gradually decreasing until no suggestion of difference is seen above 1,300 mm.

In *T. albacares* a gradual negative allometry after 600 mm. keeps the pectorals shorter than in *T. alalunga* or either Atlantic or Pacific *T. obesus* until about 1,100 mm., when overlap with *T. obesus* begins to increase.

Whereas the pectorals of *T. atlanticus* are, at first, very similar in length to those of *T. albacares*, the more rapid decline in relative length makes them at sizes above 600 mm. even shorter than in *T. albacares.*

The greatest negative allometry is seen in *T. tonggol*, which, at 500 mm., already shows the trend that brings the pectoral length into the ranges of *T. maccoyii* and *T. thynnus* between 650 and 900 mm. The fins are the shortest of all the species at fork lengths from 900 to 1,050 mm. (the maximum size of *T. tonggol* for which data were available).

Except for the size range where *T. tonggol* overlaps it, *T. thynnus* has pectorals consistently shorter than those of other species, the longest on record being about 23 percent of fork length.

Although more data are needed for *T. maccoyii*, it appears that this species has a slightly longer pectoral fin than *T. thynnus.* From 650–750 mm. fork length, for which a fair amount of data is available, the fin of *T. maccoyii* is 20–24 percent of fork length, that of *T. thynnus* 17–21 percent. A few specimens of *T. maccoyii* between 900 and 1,000 mm., and one of 1,445 mm. have pectorals 22–23 percent of fork length, also slightly longer than those of similar sized *T. thynnus.* The ranges given by Iwai, Nakamura, and Matsubara (1965: 31, 33) of 4.8–6.0 in fork length (=16.7–21.7 percent) for *T. thynnus* and 4.4–4.5 in fork length (=22.2–22.7 percent) for *T. maccoyii* suggest a distinctness of separation that is not upheld by our data, although the basic species differences in pectoral length appear to be real.

The distance from snout to second dorsal origin relative to fork length (fig. 27) shows a negative regression in all species of *Thunnus* over 400 mm. When size is taken into account, this measurement provides a reliable separation of some species, but a simple statement of range is inadequate. For example, *T. tonggol* appears distinct throughout its size range (maximum around 1,000 mm.) but larger *T. albacares*, *T. obesus*, and *T. thynnus* all have a distance that is the same as that of smaller *T. tonggol.*

Throughout the size ranges examined by us (fig. 27) the distance is greatest in *T. alalunga* and least in *T. tonggol.* Two intermediate groups can be categorized: one with a shorter distance that includes *T. atlanticus* and *T. albacares*, and one with a longer distance that includes *T. obesus* and *T. thynnus.* The meager data for *T. maccoyii* fall in the range of *T. thynnus.* Below a fork length of about 600 mm. there is so much overlap that the usefulness of snout-second dorsal distance in species distinction is doubtful, but above 600 mm. it appears to be useful.

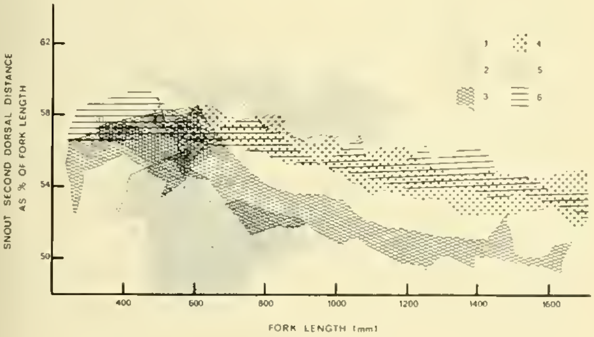


FIGURE 27.—Relative distance from snout to second dorsal origin in *Thunnus* species. Data, in additon to our own, include Dung and Royce (1953: tables 12, 21, 28, 42, 50–54). 1—*T. atlanticus;* 2—*T. tougol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

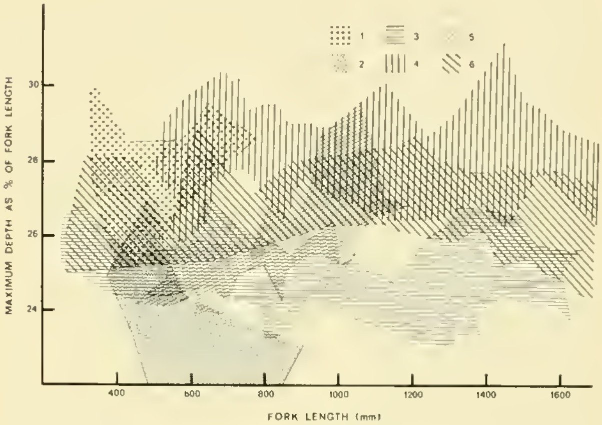


FIGURE 28.—Relative greatest body depth in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—T. *tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

Greatest body depth is shown in fig. 28. This character is so variable that it should not be used by itself. Rather, there are tendencies which, with other characters, can be helpful in species determination.

In specimens less than about 600 mm. fork length, overlap is particularly evident, but two categories can be based on greatest depth: deep-bodied species, including *T. obesus*, *T. thynnus*, and *T. atlanticus*, with depths usually 26–30 percent of fork length; and slender species, including *T. albacares*, *T. tonggol*, and *T. alalunga*, with depths usually 23–26 percent of fork length. The few data for *T. maccoyii* fall in with *T. thynnus.*

There appears to be little change in depth relative to fork length from 600 to 1,500 mm. in any species except *T. alalunga*, in which the relative depth increases gradually until specimens over 1,000 mm. are clearly in the deep-bodied category.

The two species that commonly become larger than 1,500 mm., *T. obesus* and *T. thynnus*, exhibit increased variability at these larger sizes. In *T. thynnus* this is particularly evident; specimens over 2,000 mm. fork length (not shown in fig. 28) appear randomly distributed over a range of body depths from 22–29 percent of fork length, which is almost the entire range of all species combined.

The greatest body depth is found in individuals of *T. obesus* at all sizes over 600 mm., but the species overlaps with *T. atlanticus*, *T. thynnus*, or *T. alalunga* throughout its known size range.

Eye size, in combination with other characters, is a useful species criterion, but the negative allometry must be considered. Because we measured the bony orbit, our data are not comparable with most other published data. We recommend that future workers use iris diameter.

Fig. 29 compares the species. Both *T. alalunga* and *T. atlanticus* exhibit wide variation in eye diameter, making categorical statements difficult. At less than 600 mm. fork length the smallest orbit diameter is found in *T. thynnus* and *T. tonggol*, the largest in *T. atlanticus* and *T. alalunga*, and intermediate in *T. albacares; T. obesus* is not represented.

At sizes greater than 600 mm., *T. obesus* clearly has the largest orbit diameter. Variation in *T. alalunga* covers the range from largest to smallest. The other species have so much overlap with one another that species distinctions are impossible.

COLORATION

Colors and color patterns of tunas have limited use in tuna systematics because they show great individual and age variation, and because they may be lost after death and preservation. Nevertheless, there are some excellent color characters, in spite of the difficulty in verbal expression of many of them. Many of the descriptions are taken from Mather (1964).

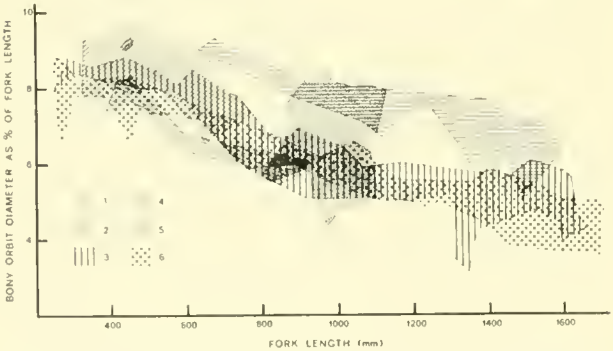


FIGURE 29.—Diameter of bony orbit relative to fork length in *Thunnus* species. Only our data used. 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

Body. Most *Thunnus* species are iridescent dark blue above and silvery below. *T. albacares* is the most brilliantly colored, with a shining golden lateral band. *T. atlanticus* also has a prominent gold lateral band, but its body is usually very dark compared with other species. *T. obesus* may display a trace of a gold band, but the band is apparently absent in *T. thynnus* and *T. tonggol* and is replaced by an iridescent blue band in *T. alalunga.*

Small specimens of all species may display a pattern of white spots or streaks ventrolaterally. In *T. tonggol* these markings consist of horizontally elongated spots. The other six species have rounded spots that are either randomly distributed or tend to become arranged in vertical rows that alternate with vertical white lines; horizontally elongated spots are sometimes seen on the caudal peduncle but rarely farther anteriorly. This pattern is usually lost in large individuals, although it may be retained in specimens of *T. albacares* and *T. thynnus* up to 1,500–1,600 mm.

In *T. maccoyii*, alone among the species of *Thunnus*, the caudal keels are an unmistakable bright yellow. In the fish markets of Japan, we were able to recognize *T. maccoyii* from a considerable distance on the basis of this character. However, we suspect the keels may lose their yellow in larger adults.

Fins. The color of the first dorsal fin is variable. It may be entirely white, or there may be a yellow suffusion, and the distal margin may be black. Too few observations have been made to enable us to characterize the species. The second dorsal and anal fins usually have yellow tips in all but *T. alalunga* and *T. atlanticus*, which have dark fins with white distal margins. The dorsal and anal finlets are usually bright yellow with black margins in all except *T. alalunga* and *T. atlanticus*. In *T. albacares* the black margin is usually very narrow, while in *T. obesus* it is wider. *T. alalunga* may have yellow in the dorsal and some anal finlets, but the anal finlets are commonly all silvery or dusky. Both the dorsal and anal finlets of *T. atlanticus* are almost invariably dusky with white margins; yellow has been observed in these finlets only in frozen specimens. June (1952b) reported black dorsal and anal finlets in an unusual specimen of *T. albacares* from the central Pacific.

The caudal fin of *T. alalunga* has a narrow, white trailing margin that distinguishes it from all other *Thunnus*, in which the white margin is lacking.

Specific Characters. The uniformly white-margined dusky finlets of *T. atlanticus*, the white caudal margin of *T. alalunga*, the horizontally elongated ventrolateral spots of *T. tonggol*, and the yellow caudal keels of *T. maccoyii* are the only color characters we regard as generally useful in distinguishing species, and confusing examples of other species with these same characters have been observed.

PART 2. SYSTEMATICS

Workers have differed in their interpretations of the suprageneric relationship of tunas and the mackerel-like fishes. Regan (1909) and Starks (1910) placed all of these fishes in the single family Scombridae. Kishinouye (1915, 1917, 1923) recognized four families: Scombridae, Cybiidae, Katsuwonidae, and Thunnidae, the last two of which he (1917, 1923) recognized as an order Plecostei, separate from the Teleostei, in which he included all other higher bony fishes. Takahashi (1924, 1926) disagreed with the recognition of a distinct order but did not alter the four families. More recently, Fraser-Brunner (1950) placed the tuna-like and mackerel-like fishes back in the Scombridae. Berg (1940, 1955) is one of the few recent taxonomists who followed Kishinouye in placing the tunas in a separate order Thunniformes. For reasons outlined elsewhere (Collette and Gibbs, 1963), we follow Regan, Starks, and Fraser-Brunner in placing all of the tunas and other mackerel-like fishes in the family Scombridae.

It is possible to divide the Scombridae into smaller units. *Gasterochisma* is so different from the other scombrids that it deserves at least subfamily status. Fraser-Brunner (1950) recognized only the subfamilies Gasterochismatinae and Scombrinae. Nakamura (1965) considered *Thunnus* and *Euthynnus* (including *Katsuwonus*) as a third subfamily, Thunninae. In the comparative diagnosis of the genus *Thunnus* which follows, we give suggestions of other possible subdivisions. Until a thorough anatomical study is completed, however, we do not wish to present formally a revised family classification.

THUNNUS SOUTH, 1845

Thynnus Cuvier, 1817: 313 (type-species: *Scomber thynnus* Linnaeus, 1758, by absolute tautonymy; preoccupied by *Thynnus* Fabricius, 1775, a genus of Hymenoptera).

Orcynus Cuvier, 1817: 314 (type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788], by subsequent designation of Jordan, 1888: 180; preoccupied by *Orcynus* Rafinesque, 1815, a substitute for *Scomberoides* Lacépède).

Thinnus S. D. W., 1837 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; suppression in favor of *Thunnus* South, 1845 requested by Collette and Gibbs, 1964).

Thunnus South, 1845 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Orycnus Cooper, 1863: 77 (substitute name for *Thynnus* Cuvier, 1817, and therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; not *Orycnus* of Gill, 1861, a misprint for *Orcynus* Cuvier, 1817).

Albacora Jordan, 1888: 180 (substitute name for *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Germo Jordan, 1888: 180 (substitute name for *Orcynus* Cuvier, 1817, therefore taking the same type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788]).

Parathunnus Kishinouye, 1923: 442 (type-species: *Thunnus mebachi* Kishinouye, 1923 [= *Thynnus obesus* Lowe, 1839], by monotypy).

Neothunnus Kishinouye, 1923: 445 (type-species: *Thynnus macropterus* Temminck and Schlegel, 1844 [= *Scomber albacares* Bonnaterre, 1788] by subsequent designation of Jordan and Hubbs, 1925: 218).

Kishinoella Jordan and Hubbs, 1925: 219 (type-species: *Thunnus rarus* Kishinouye, 1923 [= *Thynnus tonggol* Bleeker, 1851] by original designation).

Semathunnus Fowler, 1933: 163 (type-species: *Semathunnus guildi* Fowler, 1933 [= *Scomber albacares* Bonnaterre, 1788] by original designation).

Comparative Diagnosis

The tunas, genus *Thunnus*, comprise a group of seven closely related species representing the most advanced members of the family Scombridae (sensu Regan, 1909; Starks, 1910; and Fraser-Brunner, 1950). The subfamily Scombrinae of Fraser-Brunner, which includes all Scombridae except *Gasterochisma*, is divisible into two major groups (Collette and Gibbs, 1963). The more primitive *Scomber, Rastrelliger, Scomberomorus, Grammatorcynus*, and *Acanthocybium* have a posterior notch in the hypural plate and lack a bony lateral keel on the caudal vertebrae. The more advanced group, consisting of *Gymnosarda, Orcynopsis, Sarda, Cybiosarda, Auxis, Euthynnus, Katsuwonus, Allothunnus*, and *Thunnus*, lack a hypural notch and have a bony caudal keel. Within the latter group another category may be recognized as including *Allothunnus, Auxis, Euthynnus, Katsuwonus*, and *Thunnus* (the Plecostei of Kishinouye, 1917, 1923), characterized by the presence of well-developed prootic pits and (except *Allothunnus*) a subcutaneous vascular system. Within this group of higher scombrids, the genus *Thunnus* is characterized by the presence of fronto-parietal foramina, a particularly well-developed subcutaneous vascular system with two long lateral branches on each side, and the body fully covered with scales. *Auxis* and *Allothunnus* lack fronto-parietal foramina. *Auxis, Euthynnus*, and *Katsuwonus* have the body squamation limited to an anterior corselet and do not have the subcutaneous vascular system as well-developed as in *Thunnus;* the lower lateral branch is either short, or, if long as in *K. pelamis*, it meets the upper branch mesial to the ribs.

Validity of Nominal Genera

Cuvier (1817: 312–314) was the first to divide the large Linnaean genus *Scomber*. For the tunas he proposed *Thynnus* for *T. thynnus* and *Orcynus* for *T. alalunga*. Later (in Cuvier and Valenciennes, 1831) he placed his subgenus *Orcynus* in the synonymy of *Thynnus*. Several subsequent workers independently realized that *Thynnus* Cuvier was preoccupied by *Thynnus* Fabricius in insects. Thus Cooper (1863) accepted Gill's (1861) *Orycnus*, a misspelling of *Orcynus*, as a replacement name for *Thynnus* Cuvier (see also Gill, 1889). Jordan (1888) overlooked this action and proposed *Albacora* to replace *Thynnus*, and *Germo* to replace *Orcynus*. Gill (1894) settled matters by showing that South (1845) had previously suggested *Thunnus* to replace *Thynnus* Cuvier. Most subsequent workers have used *Thunnus* South either for *T. thynnus* alone or for several or all of the seven species we refer to *Thunnus*. Whitley (1955) recently discovered an earlier modification of *Thynnus* Cuvier, namely *Thinnus* S.D.W., 1837. S.D.W. (perhaps S. D. Wood, according to Whitley) emended a number of names by changing y to i, ph to f, ... As far as we can determine, only Abe (1955) followed Whitley in the usage of *Thinnus* S. D. W. In order to stabilize the consistent usage of *Thunnus* South from about 1890 to the present, we have applied to the International Commission of Zoological Nomenclature to suppress *Thinnus* S. D. W. (Collette and Gibbs, 1964).

Other nominal genera have been proposed, based on anatomical data. Kishinouye (1923) described two additional genera: *Parathunnus* based on *T. obesus* (as *mebachi*) and *Neothunnus* which included *albacares* (as *macropterus*) and *tonggol* (as *rarus*). He based this division on anatomical characters such as liver striations, the level at which the subcutaneous blood vessels pass through the myomere, and presence or absence of the postcardinal vein. Jordan and Hubbs (1925) then proposed *Kishinoella* for *T. tonggol* (as *rarus*), the only tuna that generally lacks a swim bladder. We have summarized these differences and others that have been used to distinguish genera or subgenera (table 4). A large number of different arrangements can be made depending on which characters one wishes to emphasize as "basic." *Thunnus* can be divided into two groups using the area of origin of the cutaneous artery, the level at which it passes between the ribs, and the intermuscular bones between which it divides: *T. alalunga, T. maccoyii*, and *T. thynnus* in one and *T. obesus, T. albacares, T. tonggol*, and *T. atlanticus* in the other. On the basis of number of arteriolar rows, *T. thynnus, T. maccoyii*, and *T. obesus* stand out from the other species. The presence of liver striations and vascular cones and the length of the liver lobes place *T. alalunga, T. maccoyii, T. thynnus*, and *T. obesus* in one group, the remaining three species in another. The absence of a swimbladder distinguishes *T. tonggol* from the other species, but the swimbladder may be rudimentary in *T. maccoyii*, and a swimbladder has been observed in small *T. tonggol*. *T. atlanticus* is unique in *Thunnus* in having 19 instead of 18 precaudal vertebrae. *T. atlanticus* and *T. tonggol* fall together on the basis of their low number of gill rakers, and *T. thynnus* stands out with the highest number in the genus. *T. alalunga* is unique in the position of spleen and stomach, in the shape of the first ventrally directed parapophysis,

TABLE 4.—*Comparison of diagnostic characters of the species of* Thunnus

Character	*T. alalunga*	*T. thynnus*	*T. maccoyii*	*T. obesus*	*T. albacares*	*T. atlanticus*	*T. tonggol*
Cutaneous artery orginates at vertebra number	3–4	3–4	3–4	6–8	6–8	6–8	6–8
Cutaneous artery passes between ribs number	3–4	3–4	3–4, 2–3	5–6	5–6	5–6	5–6
Cutaneous artery divides between intermuscular bones number	4–5	4–5	4–5, 3–4	6–7	6–7	6–7	6–7
Number of arteriolar rows from cutaneous artery	1	2	2	2	1	1	1
Post-cardinal vein	absent	absent	absent	present	present	present	present
Liver striations and vascular cones	present	present	present	present	absent	absent	absent
Liver lobes	subequal	subequal	subequal	subequal	right long	right long	right long
Swimbladder	present	present	present	present	present	present	absent or rudimentary
Spleen position	right	left	left	left	left	left	left
First haemal arch on vertebra number	10	10(11)	10	11(10)	11(10, 12)	11(10)	11(12)
First ventrally directed parapophysis on vertebra	9	8	9	9	9	9	10
Anterior haemal prezygapophysis position	on centrum	near centrum	near centrum	near centrum	well ventrad	well ventrad	well ventrad
Anterior haemal postzygapophysis length	short	short	short	short	long	long	long
Ventrolateral foramina size	small	small	small	small	large	large	large
Number of precaudal vertebrae	18	18	18	18	18	19	18
Posterior parasphenoid margin	angulate	angulate	angulate	angulate	non-angulate	non-angulate	non-angulate
Pectoral length	long	short	short	long to medium	medium	medium	medium to short
Gill raker number	25–31	34–43	31–40	23–31	26–34	19–25	19–28

and in the flattened haemal spine of its first caudal vertebra.

Not only is the subdivision of *Thunnus* into genera or subgenera an arbitrary matter, but such subdivision obscures the close relationship among the species. In this concept we agree with such workers as Rivas (1951, but not 1961), de Sylva (1955), and Iwai, Nakamura, and Matsubara (1965). *Thunnus* can be divided into as many as six groups, but these are essentially species, not subgenera or genera (table 4). However, based on the 18 characters in table 4 (excluding pectoral fin length), there do appear to be two groups of species. *T. alalunga*, *T. thynnus*, and *T. maccoyii* are similar to each other in 14-16 characters; *T. albacares*, *T. atlanticus*, and *T. tonggol* are similar to each other in 15-16 characters; and *T. obesus* is in between the two groups, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares*. This agrees with the intra-generic relationships presented by Iwai et al. (1965) and Nakamura (1965). It disagrees with Watson's (1964) groups where she placed *T. obesus* in the first group. *T. obesus* is similar to the first group in several liver and vertebral characters but fits with the second group in position of the cutaneous artery, presence of the post-cardinal vein, and position of the first haemal arch.

The synonymy of each species includes all the combinations of names we have found, together with selected references containing information on anatomy, morphometry, and distribution. Readers wishing more references should consult tuna bibliographies such as Corwin (1930), Shimada (1951), and volume 4 of the "Proceedings of the World Scinetific Meeting on the Biology of the Tunas and Related Species" (Bernabei, 1964).

THUNNUS ALALUNGA (Bonnaterre, 1788)
ALBACORE

Scomber pinnis pectoralibus longissimis Cetti, 1777: 191-193 (Sardinia, *alalunga* in vernacular).

Scomber alalunga Bonnaterre, 1788: 139 (original description based on Cetti). Walbaum, 1792: 222. Risso, 1810: 169-170.

Scomber alatunga Gmelin, 1789: 1330 (original description based on Cetti; "*alatunga*" a misprint for "*alalunga*"; date of publication according to Cat. Books British Mus. is 1789, not 1788). Lacépède, 1800: 599 and 1802: 21–22.

Scomber germo Lacépède, 1800: 598 (original description in table of species of *Scomber;* misspelled *S. germon*). Lacépède, 1802: 1–8 (description: S. Pacific Ocean, 17° S., 103° W.; based on Commerson's manuscript).

Orcynus germon, Cuvier, 1817: 314.

Orcynus alalonga, Risso, 1826: 419–420 (Mediterranean).

Thynnus alalonga, Cuvier *in* Cuvier and Valenciennes, 1831: 87–95 (Atlantic), fig. 215. Lowe, 1839: 78 and 1849: 2 (Madeira). Günther, 1860: 366. Cunningham, 1910: 109–110 (synonymy, description; St. Helena), fig. 3.

Thynnus pacificus Cuvier *in* Cuvier and Valenciennes, 1831: 96–97 (substitute name for *Scomber germo* Lacépède, 1800).

Thunnus alalonga, South, 1845: 622.

Thunnus pacificus, South, 1845: 622.

Orcynus pacificus (not of Cuvier) Cooper, 1863: 75–77 (original description; California), fig. 19.

Orcynus germo, Lütken, 1880: 468–472, 596 (synonymy in part), pl. 3, figs. 1–2 (young). Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo alalonga, Jordan, 1888: 180. Barnard, 1927: 799 (S. Africa). Morice, 1953: 68-69, fig. 3 (description of liver; E. Atlantic).

Albacora alalonga, Dresslar and Fesler, 1889: 438–439 (synonymy in part), pl. 6.

Germo alalunga, Jordan and Evermann, 1896: 871 (description; synonymy in part; Atlantic and Pacific). Jordan and Jordan, 1922: 33 (Hawaii). Meek and Hildebrand, 1923: 316–317 (description; synonymy in part). Jordan and Evermann, 1926: 15 (Atlantic). Buen, 1930: 48 (synonymy in part), fig. 6. Jordan, Evermann, and Clark, 1930: 260 (synonymy in part). Fowler, 1936: 621–623 (synonymy in part; description), fig. 280. Walford, 1937: 14–17 (description; a single worldwide species of albacore), color pl. 35. Fowler, 1944: 498 (W. of Chile). Tinker, 1944: 158–159 (Hawaii), pl. 1, fig. 6. Brock, 1949: 267 (in key to Hawaiian tunas). Le Gall, 1949 (synonymy, description, biology). Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835. Fernandez-Yepez and Santaella, 1956: 12, fig. 3, pls. 1, 5, (Venezuela). Tucker, 1955 (British Seas). Otsu, 1960 (migration, growth; N. Pacific). Frade and Vilela, 1962: 17–59 (morphology, biology; E. Atlantic). Postel, 1963 (description, biology; E. Atlantic).

Thynnus alalunga, Clarke, 1900 (Scotland).

Germo germon, Fowler, 1905: 761–763 (Sumatra).

Germo germo, Jordan and Seale, 1906: 228 (Samoa). Jordan and Hubbs, 1925: 217 (Japan). Jordan and Evermann, 1926: 16 (Pacific), pl. 3, fig. 1. Jordan et al., 1930: 260 (synonymy).

Thunnus alalunga, Jordan, Tanaka, and Snyder, 1913: 120 (Japan). Kishinouye, 1915: 18 (description; Japan). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part; distribution), fig. 5. Rivas, 1951: 222–223 (synonymy, description; Atlantic). de Sylva, 1955: 33 (relationships, osteology), fig. 56 (neurocranium). Bullis and Mather, 1956 (counts, measurements; key to Caribbean *Thunnus*), fig. 3. Kurogane and Hiyama, 1957b (morphometry; NW. Pacific). Gosline and Brock, 1960: 259–260 (description; Hawaii), 336–337 (synonymy), fig. 257i. Mather and Gibbs, 1957: 242–243 (39° 45′ N., 73° 00′ W.). Jones and Silas, 1960: 382–383 (Indian Ocean), fig. 9. Talbot and Penrith, 1962: 558 (S. Africa). Jones and Silas, 1963: 1790–1791 (Indian Ocean). Rodrigues Lima and Wise, 1963 (distribution; W. tropical Atlantic). Squire, 1963 (distribution; NW. Atlantic). Talbot and Penrith, 1963: 609–616 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3a (olfactory rosettes). Williams, 1964: 121 (E. Africa). Iwai et al., 1965: 3–5 (synonymy), 28–30 (description), figs. 13, 14, 15. Nakamura, 1965: 13–17, figs. 1, 2, 3A, 4, 5A (osteology). Merritt and Thorp, 1966: 377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus germo, Kishinouye, 1923: 434 (anatomy; Japan), figs. 20, 46, 52. Serventy, 1941: 23–24 (Australia), pl. 2. Godsil and Byers, 1944: 70–87 (anatomy; comparison of Pacific specimens), figs. 36–47. Godsil, 1948 (morphometric comparison of Japanese, Hawaiian, and American specimens). Alverson, 1961 (distribution; NE. Pacific). Clemens, 1961 (migration, age, growth; N. Pacific). Clemens, 1963 (migration; N. Pacific). Yoshida and Otsu, 1963 (biology; Pacific and Indian oceans). Otsu and Uchida, 1963 (migration; Pacific). Jones and Silas, 1964: 34–36 (Indian Ocean).

Germo germon steadi Whitley, 1933: 81–83 (original description; New South Wales), pl. 11, fig. 1.

Thunnus germon, Tortonese, 1939: 324–325 (W. coast S. America).

Thunnus alalunga germo, Munro, 1958: 111 (Australia).

Types of Nominal Species

Scomber alalunga Bonnaterre, 1788. No type specimens. Original description based on Cetti, 1777 (*Scomber pinnis pectoralibus longissimus*).

Scomber alalunga Gmelin, 1789. No type specimens. Original description based on Cetti, 1777. Specific name, published as *alatunga*, a misprint.

Scomber germo Lacépède, 1800. No type specimens. Original description based on manuscript by Commerson. Specific name spelled *germon* in table of species of *Scomber* (1800), spelled *germo* in description (1802).

Thynnus pacificus Cuvier, *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on Lacépède's *Scomber germo* (1800) and on Commerson's manuscript. The specimen, MNHN A. 6862, considered as the holotype by Bauchot and Blanc (1961, p. 377) and Blanc and Bauchot (1964, p. 456) is, therefore, not a type (Collette, 1966).

Orcynus pacificus Cooper, 1863. No type specimen, although mention is made of "State collection, species 1033."

Germo germon steadi Whitley, 1933. Holotype Australian Museum, Sydney, IA 2457, New South Wales, a misshapen skin, 960 mm. FL, preserved in formalin with most of the fins broken. Pectoral fin about 45 percent of fork length. Figured by Whitley (1933, pl. xi, fig. 1).

Characters

Pectoral fin very long, usually reaching nearly or quite to second dorsal finlet, usually 31 percent of fork length or longer (similar to *T. obesus*). Body depth greatest near dorsal and anal origins. A narrow white posterior margin on caudal fin. Anal finlets silvery or dusky.

Gill rakers 25–31 (similar to *T. obesus* and *T. albacares*).

Liver with striations on ventral surface, its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. obesus*). Spleen located on left side, stomach on right. Straight intestine short, the first loop located at about half to two-thirds the distance between middle liver lobe and anus. Gall bladder exposed in ventral view along right side of straight intestine. Connective tissue on dorsal wall of body cavity much thickened posteriorly. Kidney short, without posterior "tail," reaching level of vertebrae 7–9.

Cutaneous arteries usually originating at level of vertebra 3–4, passing laterally between ribs 3 and 4, and branching between intermuscular bones 4 and 5 (as in *T. thynnus* and *T. maccoyii*); no posterior commissure. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*) but from vertebral side of vessels. Post-cardinal vein absent (as in *T. thynnus* and *T. maccoyii*).

Posterior parasphenoid margin forming an acute angle (not as extreme as in large *T. thynnus* but more acute than in large *T. obesus*). Supraoccipital crest relatively slender and long, reaching at least to centrum of vertebra 3.

Anterior articulating (sphenotic) head of hyomandibula relatively long and narrow, proportion of length to least width 1.7–2.7. Metapterygoid relatively narrow, proportion of length of anteroventral margin to posteroventral margin 1.1–1.8. Quadrate relatively narrow, proportion of length to width of horizontal dorsal edge 2.1–2.7.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*), appearing twisted and not extending strongly ventrad. First closed haemal arch on vertebra 10 (as in *T. thynnus*, *T. maccoyii*, and occasionally in other species), forming an angle of 45 degrees or less with the vertebral axis. All haemal prezygapophyses arising from centra, not from haemal arches. All haemal postzygapophyses less than one-fourth centrum length. Anteriormost ventrolateral foramina small, their width not greater than basal width of haemal spine. Least height of centrum of 36th vertebra 1.1–1.7, usually 1.4–1.6, in centrum length (similar to *T. albacares*), centrum commonly tapering, with least depth at anterior end (in the other species the vertebra is of nearly equal height throughout). Haemal spine of first caudal vertebra flattened, wing-like.

Nominal Species

Although no one seems to have reported any important differences between Atlantic and Pacific populations of *T. alalunga*, at least since Jordan and Evermann (1926), many recent authors still refer to the Pacific populations as *T. germo*. Even Jordan and Evermann (1926) admitted that the slight differences they noted in body proportions and coloration would probably not be valid when more specimens were examined. Our data on *T. alalunga* confirm the view that the Atlantic and Pacific populations belong to the same species. Godsil (1948) and Kurogane and Hiyama (1958a, 1959) found slight population differences within the Pacific, but intermingling of a significant portion of the eastern and western Pacific populations of *T. alalunga* was indicated by tag returns reported by Ganssle and Clemens (1953) and Blunt (1954), and demonstrated by more recent works, including those of Otsu (1960), McGray, Graham, and Otsu (1961), Clemens (1961, 1963) and Otsu and Uchida (1963).

Range

In the western Atlantic, *T. alalunga* is known from south of New England to southern Brazil. Squire (1963) presented seven records north of 40° N., the most northerly 42°18′ N., 64°02′ W. Le Danois

(1951) reported the species off the coast of Venezuela. Rodrigues Lima and Wise (1963) reported catches from 10° N. to 32° S. off the coast of Brazil, with a concentration near 15° S. There are no records for the Gulf of Mexico. In the eastern Atlantic, it has been found from the Orkney Islands north of Scotland (Clarke, 1900; Tucker, 1955), south to Angola off west African coast (Vilela and Monteiro, 1959) and in the Mediterranean Sea. The range may extend south to South Africa, because Talbot and Penrith (1962, 1963) have found a continuous distribution around South Africa. On the other hand, the South African population may be of Indian Ocean origin.

The distribution in the Indian and Pacific oceans was mapped by Yoshida and Otsu (1963) and by Suda, Koto, and Kume (1963). *T. alalunga* is found across the Indian Ocean from East Africa to Australia between about 10° N. and 30° S. Its range in the western Pacific extends from about 45° N., off the coast of Hokkaido, south to 40° S., off the southern tip of Australia. Longline fishing has indicated a fairly continuous distribution between 30° N. and 20° S., eastward past the Hawaiian Islands. In the eastern Pacific, it is known from about 50° N., off Vancouver Island, British Columbia (Cowan, 1938; Samson, 1940), south to about 42° S. (Japan Fishery Agency, 1964, 1965).

THUNNUS ALBACARES (Bonnaterre, 1788)
YELLOWFIN TUNA

Albacores or *Thynni* Sloane, 1707: 11 (description; Madeira), fig. 1.

Scomber albacares Bonnaterre, 1788: 140 (original description based on drawing by Sloane).

Scomber albacorus Lacépède, 1800: 599 and 1802: 48–49 (substitute name for *Scomber albacares* Bonnaterre, 1788).

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831: 97–98 (original description; Atlantic and Pacific). Günther, 1860: 366.

Scomber Sloanei Cuvier *in* Cuvier and Valenciennes, 1831: 148 (original description based on Sloane).

Thynnus albacora Lowe, 1839: 77–78 (original description; Madeira) and 1849: 2 (repeat of original description). Günther, 1860: 365. Cunningham, 1910: 110–112 (synonymy, description; St. Helena), fig. 4.

Thynnus macropterus Temminck and Schlegel, 1844: 98–99 (original description; Japan), pl. 51. Kishinouye, 1915: 19 (description, anatomy; Japan), pl. 1, fig. 12.

Thunnus argentivittatus, South, 1845: 622. Rivas, 1951: 221–222 (synonymy).

Orcynus subulatus Poey, 1875: 145–146 (original description; Cuba), pl. 3, fig. 4 (head), fig. 5 (scale).

Orcynus albacora, Poey, 1875: 145.

Orcynus macropterus, Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo macropterus, Jordan and Snyder, 1901: 64 (Nagasaki). Jordan and Seale, 1906: 228 (Samoa). Jordan and Jordan, 1922: 32–33 (Hawaii).

Thunnus macropterus, Jordan et al., 1913: 121 (Japan). Kishinouye, 1915 (description, anatomy; Japan). de Beaufort, 1951: 223–225 (synonymy, description), fig. 39. Ginsburg, 1953: 8–10 (restriction of name *macropterus* to W. Pacific yellowfin).

Thunnus allisoni Mowbray, 1920: 9–10 (original description; Miami, Fla.), figure (unnumbered).

Germo argentivittatus, Nichols and Murphy, 1922: 507 (Peru).

Germo allisoni, Nichols, 1923: 3 (Christmas Island).

Neothunnus macropterus, Kishinouye, 1923: 446–448 (anatomy; Japan; placed in new genus *Neothunnus*), figs. 13, 19, 23, 45, 51. Jordan and Hubbs, 1925: 219 (Japan). Jordan and Evermann, 1926: 20–21 (description), pl. 5. Herre, 1936: 106–107 (synonymy; Galapagos, Philippines, Japan; no species differences between long- and short-finned yellowfin). Walford, 1937: 3–7 (description; Pacific Allison tuna merely old yellowfin), color pl. 33. Serventy, 1941: 25–26 (description; Australia), pl. 2. Godsil and Byers, 1944: 46–69 (anatomy; comparison of Pacific specimens), figs. 20–35, 70–76. Tinker, 1944: 159–160 (Hawaii), pl. 1, fig. 5. Godsil, 1948 (morphometry; Japan, Hawaii, E. Pacific). Schaefer, 1948 (morphometry; Pacific Costa Rica). Brock, 1949: 276 (key to Hawaiian tunas). Schaefer and Walford, 1950 (comparison of yellowfin from Angola and Pacific coast of Central America). Godsil and Greenhood, 1951 (comparison of E. and central Pacific specimens). Schaefer, 1952 (comparison of Hawaiian and W. Pacific specimens). Royce, 1953 (morphometry; Pacific; an east-west cline across the Pacific in some characters). Tsuruta, 1954 (morphometry; SW. Pacific). Schaefer, 1955 (comparisons of specimens from SE. Polynesia, Central America, and Hawaii). Tsuruta, 1955 (morphometry; southwest Great Sunda Island; yellowfins probably a single worldwide species with many sub-populations). Kurogane and Hiyama, 1957a (morphometry; equatorial Pacific). Kurogane and Hiyama, 1958b (morphometry; Indian Ocean). Munro, 1958: 111 (Australia). Nakagome, 1958 (morphometry; Indian Ocean). Broadhead, 1959 (morphometry; E. tropical Pacific). Klawe, 1959 (reidentification of juvenile called *T. thynnus* by Fowler, 1944). Gosline and Brock, 1960: 260–261 (description; Hawaii), 337 (synonymy), fig. 257j. Jones and Silas, 1960: 385–386 (Laccadive Sea, Gulf of Mannar, Ratnagiri), fig. 12. Legand, 1960 (measurements, counts; New Caledonia; east-west cline in gill rakers across Pacific). Tsuruta and Tsunoda, 1960 (morphometry; Indian Ocean). Talbot and Penrith, 1962: 558 (S. Africa). Mimura et al., 1963a (biology; Indian Ocean). Talbot and Penrith, 1963: 617–623 (description, biology; S. Africa).

Thunnus subulatus, Jordan and Evermann, 1926: 11–12 (repeat of Poey's original description). Jordan et al., 1930: 260. Ginsburg, 1953: 6–8 (synonymy, description; the name *subulatus* used for W. Atlantic yellowfin). Fernandez-Yepez and Santaella, 1956: 6 (Venezuela; in key as a species of bluefin).

Neothunnus catalinae Jordan and Evermann, 1926: 19 (original description; Santa Barbara Islands, S. California), pl. 4. Jordan et al., 1930: 260. Nichols and La Monte, 1941: 31, fig. 1.

Neothunnus albacora, Jordan and Evermann, 1926: 21–22. Frade, 1929: 235–241 (morphometry, swimbladder; Canary Islands), pl. 5, fig. 2. Buen, 1930: 49–50, fig. 8. Bini, 1931: 31–36 (morphometry; Canary Islands), figs. 12, 13. Frade, 1931a: 123–126 (synonymy, morphometry; E. Atlantic). Nichols and La Monte, 1941: 30 (synonymy in part), fig. 2. Barnard, 1948: 378–380 (S. Africa), pl. 11. Bellón and Bardán de Bellón, 1949 (morphometry; Canary Islands). Morice, 1953: 71–73, fig. 5 (liver; E. Atlantic). Postel, 1955 (biology, morphometry; E. Atlantic). Fernandez-Yepez and Santaella, 1956: 15 (in key to Atlantic tunas). Marchal, 1959 (morphometry; E. Atlantic). Vilela and Monteiro, 1959: 30–53 (morphometry; Angola). Tsuruta, 1961 (morphometry; SW. Indian Ocean). Vilela and Frade, 1963 (biology; E. Atlantic).

Neothunnus itosibi Jordan and Evermann, 1926: 22–23 (original description; Hawaii), pl. 6. Smith, 1935: 207–209 (S. Africa), fig. 4. Phillips, 1932: 231 (New Zealand). Powell, 1937: 80–81 (New Zealand), pl. 17, figs. 2, 3. Jones and Silas, 1960: 387–388 (Madras; recognized as distinct from *N. macropterus*), fig. 13.

Neothunnus albacores, Jordan and Evermann, 1926: 23–24 (description). Jordan et al. 1930: 260. Fernandez-Yepez and Santaella, 1956: 17–18 (Venezuela), fig. 6, pl. 8.

Neothunnus allisoni, Jordan and Evermann, 1926: 24 (description). Jordan et al., 1930: 260. Nichols and La Monte, 1941: 30–31 (synonymy), fig. 3. Fernandez-Yepez and Santaella, 1956: 16 (Venezuela), fig. 5, pl. 7.

Kishinoella zacalles Jordan and Evermann, 1926: 27 (original description, Honolulu fish market), pl. 7.

Semathunnus guildi Fowler, 1933: 163–164 (original description; Tahiti), pl. 12.

Semathunnus itosibi, Fowler, 1933: 164. Tinker, 1944: 160 (Hawaii).

Neothunnus argentivittatus, Beebe and Tee-Van, 1936: 184–192 (synonymy, description; West Indies), fig. 5 (copy of fig. in Cunningham), figs. 6–12 (photographs), fig. 13 (copy of fig. in Sloane). Fowler, 1944: 498 (Mexico, Ecuador, Peru).

Germo albacora, Fowler, 1936: 623-624 (synonymy, description), fig. 282. Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835.

Thunnus albacora, Tortonese, 1939: 326 (off Brazil). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144–145 (synonymy), fig. 7. Morrow, 1954: 16 (29 E. African specimens similar to Pacific specimens).

Germo itosibi, Smith, 1949, 1953: 299 (S. Africa), pl. 65, fig. 834.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949: 12–19 (original description; as *Neothunnus albacora* forma *brevipinna;* Canary Islands).

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949: 12–19 (new name for long-finned *T. albacares* of East Atlantic; as *Neothunnus albacora* forma *longipinna;* Canary Islands).

Neothunnus macropterus macropterus, Bellón and Bardán de Bellón, 1949: 15 (Pacific short-finned form; as *Neothunnus macropterus* forma *macropterus*).

Neothunnus macropterus itosibi, Bellón and Bardán de Bellón, 1949: 15 (Pacific long-finned form; as *Neothunnus macropterus* forma *itosibi*).

Neothunnus brevipinna, Postel, 1950: 67–74 (description, biology; considered a good species distinct from *N. albacora*).

Thunnus zacalles, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 146, fig. 9.

Thunnus albacares, Ginsburg, 1953: 3–6 (synonymy, description; the name *albacares* restricted to the E. Atlantic yellowfin). de Sylva, 1955: 33–40 (osteology, relationships), fig. 58 (neurocranium). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*), fig. 2. Mather and Gibbs, 1957: 242 (off New England). Rivas, 1961: 136–139 (synonymy, range). Schaefer, Broadhead, and Orange, 1963 (biology; Pacific). Squire, 1963 (distribution; NW. Atlantic). Iwai and Nakamura, 1964: 6, figs. 3G, H (olfactory rosettes). Tsuruta, 1964: 59–66 (morphometry; Pacific and Indian oceans). Williams, 1964: 115–120 (E. Africa). Iwai et al., 1965: 11–15 (synonymy), 36–38 (description), figs. 20, 21. Nakamura, 1965: 20–22, figs. 3E, 9B, 10 (osteology). Royce, 1965 (morphometry). Merritt and Thorp, 1966: 375–376 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus catalinae, Ginsburg, 1953: 8 (name used for E. Pacific yellowfin).

Neothunnus albacares, Mather, 1954: 292 (SE. of New York). Mather and Day, 1954: 184–185 (N. Brazil and W. Africa).

Thunnus albacores, Le Danois, 1954: 283–287 (history of nomenclature), 285–286 (partial synonymy), 288–294 (biology; Pacific yellowfin recognized as *Thunnus albacores* variety *argentivittatus*).

Neothunnus albacora macropterus, Schultz, 1960: 414–415 (description of Bikini and Marianas specimens), pl. 122 A.

Thunnus albacares macropterus, Jones and Silas, 1963: 1793–1794 and 1964: 40–42 (Indian Ocean).

Thunnus itosibi, Jones and Silas, 1963: 1794–1795 and 1964: 42–43 (Indian Ocean).

Types of Nominal Species

Scomber albacares Bonnaterre, 1788. No type specimens. Original description based on Sloane (1707, pp. 11–12; table 1, fig. 1).

Scomber albacorus Lacépède, 1800. Substitute name for *Scomber albacares* Bonnaterre, 1788.

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831. Syntypes MNHN A.5567 (a stuffed whole skin; collected in the Atlantic Ocean by Quoy and Gaimard) and A.5572 (a half skin, with glass eye, mounted on a board; sent by Dussumier from the Indian Ocean). A third specimen, A.5814, designated by Schaefer and Walford (1950) as lectotype, is not a syntype because it was not mentioned by Cuvier in the original description (cf. Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). We have examined both syntypes and cannot be certain what species they represent (see discussion under Nominal Species).

Scomber sloanei Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description clearly based on Sloane (1707), plate 1, fig. 1, but also referring to page 28, where Sloane refers to a different fish (*Scombrus major torosus*). Cuvier stated that *Scomber albacarus* Lacépède, 1800, is not the same as *Scomber sloanei*, because Lacépède's description refers to page 11 of Sloane. This, however, is the description of the fish, from the illustration of which Cuvier drew his description.

Thynnus albacora Lowe, 1839. No type specimens.

Thynnus macropterus Temminck and Schlegel, 1844. Original description clearly based on the specimen figured in plate 51, and not on the specimen in the Rijksmuseum van Natuurlijke Historie, Leiden, number 2552, considered by Boeseman (1947, 1964) as the holotype. In particular, Temminck and Schlegel refer to the long second dorsal and anal fins, which the presumed holotype (fork length 670 mm. as measured by Gibbs in 1962) is too small to have developed.

We believe that this specimen should not have been considered as holotype of this species. The specimen (a stuffed skin) is not a yellowfin tuna at all, but is *T. tonggol*. The pectoral fin is 22 percent of fork length and the snout to second dorsal distance is 50.7 percent, both characteristic of *T. tonggol*.

Since we do not believe this specimen was used in the original description and, therefore, is not a type, we are saved the necessity of having to consider the name *tonggol* Bleeker, 1851 as a junior synonym of *macropterus*, which has been used more often than has any other name for Pacific yellowfin tuna.

Orcynus subulatus Poey, 1875. No type specimens known to us. Original description from an 1,800-mm. specimen, of which the head is figured and might have been saved.

Thunnus allisoni Mowbray, 1920. No type specimen known to us. Original description from three specimens: one taken by spearing in Biscayne Bay, Miami, Fla. for which counts, proportions of body parts, and color are given, but the length noted as a little larger than the second specimen; a second specimen, 5 feet 9 inches long (1,753 mm.), "taken in the Gulf Stream," but "badly torn by sharks"; and a third specimen weighing 135 pounds (61 kg.).

Neothunnus catalinae Jordan and Evermann, 1926. Type originally designated as "No. 597, Mus. Calif. Acad. Sci., a photograph of a fish taken off Santa Catalina Island, California," weight 157½ pounds (71 kg.). This photograph was published earlier as *Germo macropterus* by Jordan and Starks (1907: 69). The fish appears to be a mounted specimen.

Neothunnus itosibi Jordan and Evermann, 1926. Type originally designated as "No. 598, Mus. Calif. Acad. Sci., a photograph . . . of a specimen weighing 321 pounds in Honolulu market." The specimen is no longer extant.

Kishinoella zacalles Jordan and Evermann, 1926. Type originally designated as "No. 599, Mus. Calif. Acad. Sci., a photograph of a specimen examined in the Honolulu market . . ., 2¼ feet long, . . . weighing 14 pounds." The characters given in the key to species (p. 26) are based on the specimen photographed; the text description is based on another specimen. Jordan and Evermann described *zacalles* as lacking a swimbladder, and they and subsequent workers (Serventy, 1942; Fraser-Brunner, 1950) have placed it close to *T. tonggol*. Jordan and Evermann, however, gave for their *zacalles* a gill-raker count of 30, which is completely outside the known range for *T. tonggol* (19–28, Table 2). It is our experience that the swimbladder may be quite difficult to find in some specimens of most species of *Thunnus*, and we believe that Jordan and Evermann probably overlooked it in their specimens of *zacalles*. They can not have been describing *T. thynnus*, as this species has more gill rakers and a much shorter pectoral fin than they show in their photograph of *zacalles*. Of the three remaining Pacific species, *T. alalunga* may be quickly eliminated because it has a much longer pectoral fin and an entirely different coloration. *T. obesus* has a much larger eye than that shown for *zacalles*, and the swimbladder is well developed in all specimens that we observed. The description of *Kishinoella zacalles* fits *T. albacares* in number of gill rakers (mean for Pacific *T. albacares* 30.2, table 2), length of pectoral fin, coloration, and general body proportions. Also, Jordan and Evermann, in their original description, reported about a dozen specimens of *zacalles*, all from Hawaii, and no specimen of it (or of *T. tonggol*) has since been reported from there. In view of the great fishery and research program on tunas in the Pacific, it seems highly unlikely that a valid species has been overlooked.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949. No type specimens. Original description based on 11 specimens from the Canary Islands.

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949. No type specimens. Presumed to be a new subspecific designation for the typical subspecies of *N. albacora* Lowe (1839).

Semathunnus guildi Fowler, 1933. Holotype ANSP 55982, a dried skin with skull intact, from Tahiti. Fowler stated, "Length 1,830 mm." Our measurement of fork length was about 1,460 mm., of length to end of caudal lobes about 1,680 mm. The specimen is obviously a yellowfin tuna, with high dorsal and anal fins, and the pectoral reaching to the middle of the second dorsal base.

Characters

Pectoral fin intermediate in length, usually reaching beyond second dorsal origin but not beyond end of its base, usually 22–31 percent of fork length (generally similar to *T. atlanticus* and large *T. obesus*). Dorsal and anal fins very long in large specimens, becoming well over 20 percent of fork length.

Gill rakers 26–35 (overlapping with *T. alalunga* and *T. obesus*).

Liver without striations on ventral surface, its right lobe longer and narrower than the others; vascular cones not present on dorsal side (as in *T. atlanticus* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Connective tissue on dorsal wall of body cavity thickened at anterior end to form a prominent raised cord. Kidney long, tapering, reaching level of vertebra 12–14, often with accessory masses posterior to main kidney.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, and branching between intermuscular bones 6 and 7 (as in *T. atlanticus* and *T. tonggol*) or 7–8. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. alalunga*, *T. tonggol*, and *T. atlanticus*) but from lateral sides of vessels (as in *T. tonggol* and *T. atlanticus*). Vessels present on each side parallel to dorsal aorta connecting posterior epibranchial to cutaneous artery. Postcardinal vein present, joining right cutaneous vein (as in *T. atlanticus*, *T. tonggol*, and *T. obesus*).

Posterior parasphenoid margin variable in shape, rounded, concave, or somewhat angulate (as in *T. atlanticus* and *T. tonggol*) but never with a pronounced angle.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all *Thunnus* except *T. thynnus* and *T. tonggol*). First closed haemal arch usually on vertebra 11 (as in *T. atlanticus*, *T. tonggol*, *T. obesus* and often in *T. thynnus*). Anteriormost haemal prezygapophyses arising far ventrad on haemal arch (as in *T. atlanticus* and *T. tonggol*). Haemal postzygapophyses long (as in *T. atlanticus* and *T. tonggol*), the longest about 75 percent of its centrum length (somewhat shorter than in *T. atlanticus* and *T. tonggol*). Anteriormost ventrolateral foramina large, their width three or more times that of haemal spine (as in *T. atlanticus* and *T. tonggol*). Least height of centrum of 36th vertebra 1.2–1.9, usually 1.3–1.5 in centrum length (resembling *T. alalunga*, but in that species the vertebrae taper, whereas in *T. albacares* they are of nearly equal width throughout).

Nominal Species

More names have been proposed for supposedly different populations and individual variants of *T. albacares* than for all other species in the genus. Jordan and Evermann (1926) took the most extreme position in recognizing seven species: *catalinae*, from the California coast; *macropterus*, from the central and western Pacific; *itosibi*, a long-finned form from Hawaii and Japan; *albacora*, from the eastern Atlantic; *albacores*, from Madeira and the West Indies; *allisoni*, a western Atlantic long-finned form; and *zacalles* from Hawaii (which has heretofore been considered as most closely related to *T. tonggol*, see above). The main characters that they used to separate these forms were the lengths of the second dorsal and anal lobes. Using the same characters, Ginsburg (1953) distinguished an eastern Atlantic *albacares*, a western Atlantic *subulatus*, an eastern Pacific *catalinae*, and a central and western Pacific *macropterus*. It became apparent to us that *T. albacares* is an extremely variable species morphometrically, from our own data and from the many detailed morphometric studies on populations of *T. albacares*, especially in the Pacific, by workers such as Godsil (1948), Schaefer (1948, 1952, 1955), Schaefer and Walford (1950), Godsil and Greenhood (1951), Royce (1953), Tsuruta (1954, 1955, 1961), Kurogane and Hiyama (1957a, 1958b), Nakagome (1958), Broadhead (1959), Legand (1960), and Frade (1931a, for the eastern Atlantic).

Statistical analysis of morphometric data indicates that many subpopulations of *T. albacares* are differentiated, but certainly not to a species or subspecies level. Royce (1965), in a monumental study of the morphometry of *T. albacares*, showed conclusively that it is a single, locally variable, pantropical species. He found that the differences between eastern Atlantic and eastern Pacific specimens were less than the differences between eastern Pacific and Caroline Islands specimens, and that several characters change clinally from west to east in the equatorial Pacific.

There has been considerable confusion concerning the name *Thynnus argentivittatus* Cuvier. The original description (Cuvier, *in* Cuvier and Valenciennes, 1831: 97–98) was based on two specimens now at the MNHN in Paris: one from the Atlantic, collected by Quoy and Gaimard (MNHN A.5572) and one from the Indian Ocean, sent by Dussumier (MNHN A.5567). Schaefer and Walford (1950) reported that, according to information received from L. Bertin, the description was based on three specimens: the two already mentioned and a third from the Indian Ocean, coast of Malabar, sent by Dussumier (MNHN A.5814; given erroneously as A.5816 by Schaefer and Walford). A.5814, a specimen in alcohol, was designated the lectotype by Schaefer and Walford (1950, p. 411), who thus recognized the Indian Ocean yellowfin as *Neothunnus argentivittatus*, the Pacific form as *N. macropterus*, and the Atlantic form as *N. albacora*. Based on A.5814 being the lectotype, Rivas (1961) used the name *argentivittatus* for an Indian Ocean tuna which he tentatively placed in the subgenus *Parathunnus*, and regarded as different from *Neothunnus albacares*, the yellowfin tuna, which he considered to be a single, pantropical species.

We have examined the supposed lectotype (A.5814) and believe it, and the other specimens in Rivas' (1961) account, actually to be *T. tonggol*. Watson (1961) reached the same conclusion, and suggested that *T. argentivittatus* be synonymized with *T. tonggol*. This action, to begin with, is inappropriate, for *argentivittatus* has priority over *tonggol*. A.5814, however, cannot be considered as the lectotype of *Thynnus argentivittatus*, as it is nowhere mentioned by Cuvier in the original description, whereas the two proper syntypes are noted (Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). The lectotype must be selected from A.5567, a stuffed whole specimen, and A.5572, a dried half specimen mounted on a board. Although both of us examined the two syntypes and independently made counts and measurements, we do not feel that we can make a selection. Even if the appropriate measurements could be considered accurate, which they certainly cannot, they do not indicate that the syntypes are *T. albacares*, but rather leave the possibility that they could be *T. tonggol* or *T. atlanticus*. The distance from snout to second dorsal origin appears to eliminate *T. thynnus*, *T. alalunga*, and *T. obesus* from consideration. We do not believe that these specimens can be definitely identified, unless a new and better character is found.

Range

As Royce (1965) has shown, *T. albacares* is a pantropical species. In the western Atlantic, it is known from about 42° N. (Squire, 1963) south through the Sargasso Sea to the Gulf of Mexico and the Caribbean Sea (Wathne, 1959) and off the coast of South America from about 10° N. to 32° S. (Rodrigues Lima and Wise, 1963). In the eastern Atlantic, it is recorded from the coasts of Spain and Portugal south to Angola (Vilela and Monteiro, 1959; Vilela and Frade, 1963) but not from the Mediterranean Sea. Talbot and Penrith (1962, 1963) have shown that *T. albacares* has a continuous distribution around South Africa, but the origin of these fish is uncertain.

It is abundant in East African waters (Williams, 1964) and is known from 20° N. to 30° S. in the Indian Ocean (Mimura et al., 1963a). In the western Pacific *T. albacares* occurs from 40° N., off the coast of Japan, to 30° S., off the coast of Australia, between the 70° F. September isotherm to the north and 75° F. February isotherm to the south (Schaefer et al., 1963). The distribution extends across the Pacific in a broad belt from about 30° N. to 20° S., between the same isotherms, and as far as 40° S. (Japan Fishery Agency, 1965).

THUNNUS ATLANTICUS (Lesson, 1830)
BLACKFIN TUNA

Thynnus atlanticus Lesson, 1830: 165–166 (original description; Trinidade Is. off Brazil). Günther, 1860: 362 (in footnote as dubious species).

Thynnus coretta Cuvier *in* Cuvier and Valenciennes. 1831: 102–104 (original description; Martinique). Günther, 1860: 363.

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831: 136–137 (original description based on Lesson's unpublished drawing).

Thunnus balteatus, South, 1845: 622.

Thunnus coretta, South, 1845: 622 (description). Jordan and Evermann, 1926: 11 (description). Jordan et al., 1930: 260.

Orcynus balteatus, Poey, 1868: 361–362 (Cuba). Poey, 1875: 145 (Cuba).

Parathunnus rosengarteni Fowler, 1934: 354, 356 (original description; Key Largo, Fla.), figs. 3–5.

Parathunnus ambiguus Mowbray, 1935 (original description; Bermuda).

Parathunnus atlanticus, Beebe and Hollister, 1935: 213–214 (Union Is., British West Indies). Beebe and Tee-Van, 1936: 178–184 (synonymy, description; Bermuda and West Indies), figs. 1–4. Fowler, 1944: 102–103 (synonymy, description; W. Caribbean), fig. 149. Schuck and Mather, 1951: 248 (N. Carolina). Mather and Schuck, 1952: 267 (Martha's Vineyard; NW. Caribbean). Mather and Day, 1954: 183–184 (off coasts of Brazil and Bermuda).

Thunnus atlanticus, Rivas, 1951: 219–220 (synonymy, description). de Sylva, 1955 (osteology, relationships, generic status), figs. 1–54, 57 (osteology). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*). Rivas, 1961: 129–131 (synonymy, description). Iwai et al., 1965: 15–16 (synonymy), 38–39 (description), fig. 22. Nakamura, 1965: 23–24, figs. 3F, 9C, 11 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Misidentifications

The specimen reported as *Parathunnus obesus* by Beebe and Tee-Van (1928: 100) from Haiti is *T. atlanticus* as they (Beebe and Tee-Van, 1936: 181) later pointed out. Fernandez-Yepez and Santaella (1956: 19) reported specimens from Venezuela as *Parathunnus obesus*, but these are probably *T. atlanticus* as indicated by Rivas (1961: 130).

The International Game Fish Association (1965) listed the world record *T. atlanticus* as a 44 pound, 8 ounce, specimen from Cape Town, South Africa. This record is obviously in error and has been corrected (1966).

Types of Nominal Species

Thynnus atlanticus Lesson, 1830. No type specimens. Original description based on a specimen 28 inches total length (711 mm.), with a pectoral fin 6 inches long (152 mm.). Subtracting 50 mm., we obtain a fork length of about 660 mm. The pectoral is about 23 percent of fork length; too short for either *T. albacares* or *T. atlanticus* (see fig. 26), but is nearer the latter. Lesson mentioned only two other characters useful in identifying the species: a coppery-red lateral band, and blue-slate colored fins (presumably also finlets). These appear sufficient to associate the name *atlanticus* with the blackfin tuna, and we follow Beebe and Tee-Van (1936) and later authors in doing so.

Scomber coretta Cuvier, 1829. No type specimen. The first use of the name *coretta* for a tuna is usually credited to Cuvier *in* Cuvier and Valenciennes (1831), where he described *Thynnus coretta*. The original description, however, consists of a footnote on page 198 of the second edition of Règne Animal (1829), which refers only to Sloane (1707, vol. 1, plate 1, fig. 3). Sloane's figure is of "*Scomber Major torosus*," and there is no way of associating it with any known species, but this indication prevents the name from being considered a nomen nudum. *Scomber coretta* Cuvier, 1829 must be regarded as a nomen dubium.

Thynnus coretta Cuvier *in* Cuvier and Valenciennes, 1831. This later use of the name *coretta* is based on a preserved specimen, MNHN A.5380, 263 mm. fork length from Martinique. It is a blackfin tuna with 19+20 vertebrae and a gill-raker count of 6+17 (left) and 7+17 (right).

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on an unpublished illustration by Lesson of the same specimen from which *Thynnus atlanticus* was described, and, therefore, a synonym of that species.

Parathunnus rosengarteni Fowler, 1934. Holotype ANSP 60174, a stuffed skin 629 mm. fork length. A count of gill rakers was impossible, but our measurements show the pectoral fin to be 25.8 percent of fork length, characteristic of *T. atlanticus*.

Parathunnus ambiguus Mowbray, 1935. No type specimens. Original description based on Bermuda specimens; gill rakers noted as 6+17, swimbladder "simple, broader than long, well forward," finlets dusky with a trace of yellow. These characters unquestionably refer this nominal species to the synonymy of *T. atlanticus*.

Characters

Pectoral fin intermediate in length (generally similar to *T. albacares* and large *T. obesus*), usually 22–31 percent of fork length. Dorsal and anal finlets in fresh specimens lacking yellow.

Gill rakers 19–25, resembling only *T. tonggol*.

Liver without striations on ventral surface, right lobe long and narrow, no vascular cones on dorsal surface (as in *T. albacares* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*).

Swimbladder either small, oblate, situated far anteriorly, or resembling a poorly developed *T. albacares;* when long, anterior and posterior chambers divided by a membrane.

Cutaneous arteries usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares*, *T. tonggol*, and *T. obesus*). A single row of arterioles and venules arises from each main lateral cutaneous branch (as in *T. albacares*, *T. tonggol*, and *T. alalunga*), but from the lateral side of each vessel (as in *T. albacares* and *T. tonggol*). Postcardinal vein present, joining right cutaneous vein (as in *T. albacares*, *T. tonggol*, and *T. obesus*).

Posterior parasphenoid margin rounded, concave, or somewhat angulate (as in *T. albacares* and *T. tonggol*), never with a pronounced angle. Parasphenoid concave in its anterior portion (seen occasionally in small specimens of all other species).

Vertebrae 19+20, with rare exceptions. First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in all except *T. alalunga* and some *T. thynnus*). Haemal arches narrow, bowing widely, forming a large, ovate canal (as in *T. tonggol*). Anterior haemal prezygapophyses arising far ventrad on haemal arch (as in *T. tonggol* and *T. albacares*). Longest haemal postzygapophyses equal to or longer than centrum (only *T. tonggol* and *T. albacares* approach this). Anteriormost ventrolateral foramina large, more than three times width of haemal spine (as in *T. albacares* and *T. tonggol*).

Nominal species

Beebe and Tee-Van (1936) established the validity of *T. atlanticus* and placed *Thynnus balteatus*, *Para-*

thunnus rosengarteni, and *P. ambiguus* in its synonymy. *Thynnus coretta*, which was placed in the synonymy of *T. thynnus* by Fraser-Brunner (1950) and Rivas (1951), is also a synonym of *T. atlanticus*, as Rivas (1961) has recently shown. Morice (1953), Frade (1960), and others have mistakenly plac *Ted. atlanticus* in the synonymy of *T. obesus*.

Range

Thunnus atlanticus is known only from the western Atlantic, from off Martha's Vineyard, Mass. (Mather and Schuck, 1952), and Cape Hatteras (Schuck and Mather, 1951), throughout the West Indies (Beebe and Tee-Van, 1936) and the northern Caribbean (Bullis and Mather, 1956), south to Trinidade Island off the coast of Brazil (Lesson, 1830) and off Rio de Janeiro at 22°21′ S., 37°37′ W. (Mather and Day, 1954).

THUNNUS OBESUS (Lowe, 1839)
BIGEYE TUNA

Thynnus obesus Lowe, 1839: 78 (original description; Madeira). Lowe, 1849: 2 (copy of original description). Günther, 1860: 362 (in footnote as dubious species). Cunningham, 1910: 112 (synonymy, description; St. Helena), fig. 5.

Thynnus sibi Temminck and Schlegel, 1844: 97–98 (original description; Japan), pl. 50. Günther, 1860: 362 (in footnote as dubious species).

Orcynus sibi, Kitahara, 1897: 1–2 (description; Japan), pl. 1, fig. 2.

Thunnus sibi, Jordan and Snyder, 1901: 64 (*Germo sibi;* Nagasaki), 125 (supplementary note: the "Shibi" should be a species of *Thunnus*, *T. sibi*). de Beaufort, 1951: 222–223 (synonymy, description). de Sylva, 1955: 34–40 (osteology, relationships), fig. 59 (neurocranium). Rivas, 1961: 135–136 (synonymy, description; a valid Indo-Pacific species).

Germo sibi, Jordan and Snyder, 1901: 64 (listed; in supplementary note, p. 125 as *Thunnus sibi*). Jordan and Jordan, 1922: 33 (Hawaii).

Thunnus mebachi Kishinouye, 1915: 19 (original description; Japan).

Parathunnus mebachi, Kishinouye, 1923: 442–445 (description, anatomy; placed in the new genus *Parathunnus*), figs. 4, 22, 47, 49. Godsil and Byers, 1944: 104–119 (anatomy; E. Pacific). Mimura et al., 1963b (biology; Indian Ocean).

Parathunnus sibi, Jordan and Hubbs, 1925: 218 (description; Japan). Jordan and Evermann, 1926: 17 (description), pl. 3, fig. 2. Tinker, 1944: 159 (Hawaii). Brock, 1949 (description; Hawaii). Shimada, 1954 (distribution in Pacific). Gosline and Brock, 1960; 261 (description; Hawaii), 337 (synonymy). Alverson and Peterson, 1963 (biology; Pacific).

Parathunnus obesus, Jordan and Evermann, 1926: 17 (description). Frade, 1929: 229–235 (morphometry, swimbladder; Canary Is.), pl. 5, fig. 1. Buen, 1930: 50, (Spain) fig. 9. Bini, 1931: 27–30 (morphometry; Canary Is.). Frade, 1931a (morphometry, swimbladder; E. Atlantic). Beebe and Tee-Van, 1936: 181 (comparison with *T. atlanticus*). Morice, 1953: 70–71, fig. 4 (liver; E. Atlantic.) Frade, 1960: 1–74 (description, distribution, biology, bibliography), pl. 1–7.

Thunnus obesus, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144 (synonymy, in part), fig. 6. Rivas, 1951: 220 (comparison with *T. atlanticus* and *T. alalunga*). Bullis and Mather, 1956 (counts, morphometry, key to Caribbean species of *Thunnus*), fig. 2. Mather and Gibbs, 1958: 23 (NW. Atlantic). Rivas, 1961: 133–135 (description, synonymy; restricted to Atlantic). Talbot and Penrith, 1961: 240 and 1962: 558 (S. Africa). Talbot and Penrith, 1963: 624–629 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3B (olfactory rosettes). Iwai et al., 1965: 9–11 (synonymy), 34–36 (description), fig. 19. Nakamura, 1965: 18–19, figs. 3D, 8, 9A (osteology). Merritt and Thorp, 1966: 376–377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Parathunnus obesus mebachi, Jones and Silas, 1960: 383–384 (Indian Ocean), fig. 10.

Thunnus obesus sibi, Jones and Silas, 1963: 1791–1792 (Indian Ocean).

Thunnus obesus mebachi, Jones and Silas, 1964: 36–38 (Indian Ocean).

Misidentification

The 1,450-mm. specimen reported as *T. thynnus* by Fernandez-Yepez and Santaella (1956) is probably *T. obesus* as indicated by Mather and Gibbs (1958: 238) and by Rivas (1961: 134).

Types of Nominal Species

Thynnus obesus Lowe, 1839. No type specimens. Original description rather vague, but definitely referring to the species as now recognized. Apparently based on large specimens from Madeira. Differentiated from *T. thynnus* (as *Thynnus vulgaris*) "by the larger eye and shorter thickset figure." Pectoral fins described as reaching end of second dorsal fin, longer than in *T. albacares* (as *Thynnus albacora*).

Thynnus sibi Temminck and Schlegel, 1844. Lectotype, RMNH 2327 (a mounted skin, 600 mm. fork length), and paralectotype, RMNH 799 (right side of mounted skin, backed by cardboard, 557 mm. fork length) designated by Boeseman (1947). Measurements made by Gibbs in 1962 fall in the range of *T. albacares* rather than *T. obesus*, but mounted specimens could be expected to be unreliable for this purpose. The description by Temminck and Schlegel likewise offers little aid in identifying the species. They note that the pectoral fin is shorter than in *T. alalunga* (as *Thynnus alalonga* or *T. pacificus*) and approaches in length that of *T. albacares* (as *T. argentivittatus*), and their illustration shows a pectoral fin resembling that of a fairly small Pacific *T. obesus*. On this basis, we follow other authors in considering *T. sibi* a synonym of *T. obesus*. If the measurements of the lectotype and paralectotype were taken at face value, *T. sibi* would have to be regarded as a synonym of *T. albacares*, but we prefer for the present to disregard these specimens.

Thunnus mebachi Kishinouye, 1915. No type specimens. Original description clearly referable to *T. obesus*, apparently based on a number of specimens.

Characters

Pectoral fin intermediate in length (22–31 percent of fork length) in specimens longer than 1,100 mm. (as in *T. albacares* and *T. atlanticus*), as long as in *T. alalunga* (greater than 31 percent) in specimens less than 1,100 mm. from the Pacific.

Gill rakers 23–31 (generally similar to *T. albacares* and *T. alalunga*).

Liver with striations on ventral surface (not restricted to margins, fig. 30), its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Swimbladder as long as body cavity, with two globular dorsal heads anteriorly, tapering gradually to a point posteriorly. Kidney with a short tail, reaching the level of vertebra 11–13.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. thynnus* and *T. maccoyii*). Post-cardinal vein present, joining right cutaneous vein (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*).

Posterior parasphenoid margin either rounded (in some small specimens) or forming a slightly obtuse angle (not as acute as in *T. alalunga*, *T. maccoyii*, or *T. thynnus*).

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in *T. albacares*, *T. atlanticus*, *T. tonggol*, and some *T. thynnus*). Haemal prezygapophyses arising high on haemal arch (as in *T. thynnus* and *T. maccoyii*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*). Anteriormost ventrolateral foramina small, not more than 1½ times width of haemal spine (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*).

Nominal species

Three names have been applied to this species: *Thunnus obesus* for the Atlantic population and *T. sibi* and *T. mebachi* for the Pacific population, both latter names based on Japanese specimens. Fraser-Brunner (1950) correctly placed *sibi* and *mebachi* in the synonymy of *T. obesus* but also mistakenly included *Thunnus maccoyii*, *T. phillipsi* (= *T. maccoyii*), and *Parathunnus rosengarteni* (= *T. atlanticus*) as was pointed out by Rivas (1961). Jones and Silas (1960) stated that they could find no notable differences between Atlantic and Pacific populations, but referred to their Indian Ocean specimens as *Parathunnus obesus mebachi*. Because the name *sibi* has priority over *mebachi*, this should be *T. obesus sibi* if the Indo-Pacific population is subspecifically differentiated, and the latter name was used by Jones and Silas (1963).

Rivas (1961) claimed that the Pacific populations ("*sibi*") can be distinguished from the Atlantic *T. obesus* at lengths of about a meter by a much longer pectoral fin, but admitted difficulty in differentiating large specimens. His conclusion was based on a single small Atlantic specimen (746 mm., pectoral 29.4 percent of fork length) and 10 small specimens (data from Dung and Royce, 1953: 74) from the western Marshall Islands (600–835 mm., pectoral 38.8–44.9 percent).

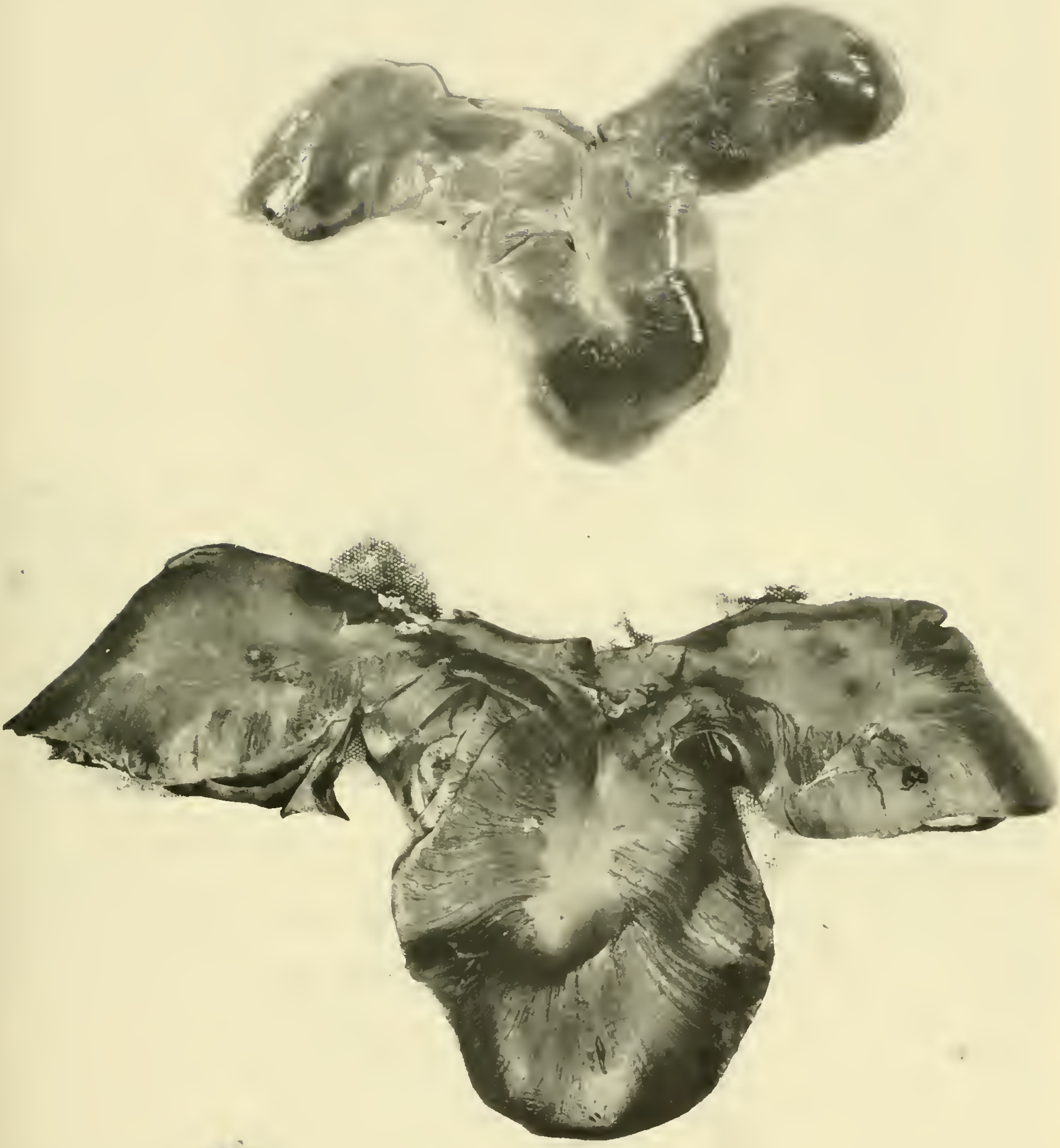


Figure 30.—Livers of Atlantic *Thunnus obesus*, ventral view. (Top) from specimen 715 mm. fork length; (bottom) from specimen 1,433 mm. fork length (photographed by P. C. Wilson).

Although abundant data are available for Pacific *T. obesus* from 400 mm. and up (Dung and Royce, 1953), very few Atlantic specimens smaller than 1,000 mm. have been recorded. These data, nevertheless, indicate that the pectoral fin in Atlantic *T. obesus* does not become as long as that of the Pacific populations and that, in fact, the length of this fin in Atlantic *T. obesus* approaches *T. albacares* more closely than Pacific *T. obesus* at intermediate sizes (650–1,000 mm). Some Pacific and Indian Ocean specimens, however, have shorter pectorals than the majority and overlap with Atlantic specimens (fig. 31).

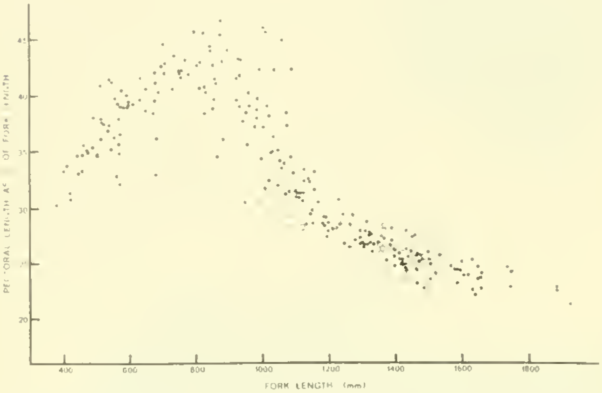


Figure 31.—Relative length of pectoral fin in *Thunnus obesus*. Dots, Indian and Pacific ocean specimens; open circles, Atlantic specimens.

It seems, therefore, that the Atlantic population of *T. obesus* is differentiated from the Pacific population, perhaps on a subspecific level, but much more data on sizes smaller than 1,000 mm. will be necessary to establish the level of differentiation.

Range

The distribution of *T. obesus* in the western Atlantic, as summarized by Mather and Gibbs (1958), includes the area from 42°18′ N., 64°02′ W. south along the coast of the United States to Florida; Bermuda; the Caribbean Sea around the West Indies; south to Margarita Island, Venezuela (reported as *T. thynnus* by Fernandez-Yepez and Santaella, 1956, but considered to be *T. obesus* by Mather and Gibbs). Nagai and Nakagome (1958) reported *T. obesus* from the north equatorial and Brazil currents off the coast of South America. In the eastern Atlantic it has been taken off Portugal, Spain, the Azores, and Madeira, south to Angola (Vilela and Monteiro, 1959) but it is absent from the Mediterranean Sea. There is a report of its occurrence from the Gulf of Gascogne (Legendre, 1936), but this needs confirmation. Talbot and Penrith (1961, 1962, 1963) have shown the distribution to be continuous around the tip of South Africa, but the fish could originate either in the Atlantic or Indian ocean.

T. obesus, like *T. albacares*, is found throughout the Indian Ocean from 20° N. to 30° S. (Mimura et al., 1963b). Its range in the western Pacific is also similar to that of *T. albacares*, extending from about 40° N. to about 30° S. (Alverson and Peterson, 1963). In the eastern Pacific it extends to 40° S. (Japan Fishery Agency, 1965).

THE BLUEFIN TUNA COMPLEX: *T. MACCOYII* AND *T. THYNNUS*

In recent years, various authors have attempted to recognize as distinct species the populations of bluefin tuna in Japan and the western Pacific (*T. orientalis*), Australia (*T. maccoyii*), eastern Pacific (*T. saliens*), western Atlantic (*T. secundodorsalis*), and eastern Atlantic (*T. thynnus*). Frade (1925) noted that the eastern Atlantic form had two rows of cutaneous arterioles, whereas Kishinouye (1923) pictured a single row in his Japanese specimen. Godsil and Byers (1944) found California bluefin similar to Kishinouye's descriptions of the form, except for two major characters. According to Kishinouye, the swimbladder of the Japanese form is short, broad, and heart-shaped, whereas that of California specimens "is rudimentary and of a different shape in small fish, and so erratic in large specimens that no constant pattern is discernible" (Godsil and Byers, 1944: 102). In California specimens, there are two rows of cutaneous arterioles and, according to Kishinouye, but a single row in Japanese fish. Godsil and Holmberg (1950) described numerous anatomical differences among California, Australian, and western Atlantic specimens, finally concluding that the Australian form (*T. maccoyii*) is distinct from the California and western Atlantic forms (*T. thynnus*) and that the latter are also distinct, but not quite so trenchantly. On the basis of published accounts of Japanese and eastern Atlantic populations (Kishinouye, 1923; Frade, 1925), Godsil and Holmberg tentatively concluded that eastern and western Atlantic forms are conspecific but that the Japanese form is different. On the basis of counts and measurements, Ginsburg (1953) recognized as species the eastern Atlantic, western Atlantic, and eastern Pacific populations but did not consider those from other geographic regions. Serventy (1956a) recognized only a single worldwide species, pointing out the ontogenetic increase in relative size of the swimbladder and suggesting that other distinguishing characters shown by Godsil and Holmberg (1950) may also be eliminated when size differences are considered. Serventy (1956a) suggested, however, that the populations from European seas, North American Atlantic coast, South Africa, North American Pacific coast, Asiatic coast of the North Pacific, and Australia-New Zealand, respectively, each be recognized as subspecies, largely on the basis of modal differences in gill-raker counts. We have previously recognized a single species with only two subspecies (Collette and Gibbs, 1963). Iwai et al., (1965) considered *T. maccoyii* and *T. thynnus* as distinct species, with no commitment as to subspecies of the latter.

When individual and ontogenetic variations are considered, almost every anatomical, morphometric, and meristic character has proved to be similar in all populations. The only exceptions are the number of gill rakers, length of pectoral fin, a few skeletal characters, the shape of the dorsal wall of the body cavity, and the color of the caudal peduncle keels. On the basis of these characters, we tentatively recognize two species of bluefin tuna: *T. maccoyii*, mainly from the Southern Ocean south of about 30° S., but including an area off northwestern Australia; and *T. thynnus*, with one subspecies, *T. t. thynnus*, in the Atlantic, and another, *T. t. orientalis* in the Pacific.

We were long reluctant to recognize *T. maccoyii* as a separate species, and even now we do so only with reservation. The only convincing characters that provide evidence of species status are the position of the first ventrally directed parapophysis (on the 9th vertebra in *T. maccoyii*, as opposed to the 10th, in *T. thynnus*) and the color of the fleshy caudal keels (yellow in *T. maccoyii*, dark in *T. thynnus*). The few other characters, none of them affording complete separation, are given in table 5.

The presence of *T. thynnus orientalis* in the southeastern Pacific and the northeastern Indian Ocean (Nakamura and Warashina, 1965), and of *T. thynnus thynnus* off Cape Town (Talbot and Penrith, 1963) in the same geographical areas as *T. maccoyii* gives biological support to considering *T. maccoyii* as a separate species, although it is not known whether the two actually spawn in the same areas.

Differences in the configuration of the dorsal wall of the body cavity are not apparent in specimens less than about 1,300 mm. As described by Godsil and Holmberg (1950), numerous western Atlantic specimens (*T. t. thynnus*) examined by us in the field and laboratory had a wide anterior bulge without a lateral concavity and had a deep, narrow trough lateral to the bulge (fig. 32). Our only large specimen of *T. maccoyii* (1,450 mm.) was similar to the western Atlantic forms. Eastern Pacific specimens of *T. t. orientalis*, 1,390 and 1,450 mm., confirm the differences described by Godsil and Holmberg. The anterior bulge is comparatively narrow, with a lateral concavity, and with a wide trough lateral to the bulge (fig. 32). Although we have dissected no large Japanese specimens, we are confident they will resemble those from the eastern Pacific.

Godsil and Holmberg (1950) eliminated a large number of characters from systematic consideration. We can substantiate almost all of their conclusions, and our observations invalidate most of their remaining differential characters.

The tubules of the caecal mass of *T. t. thynnus* and *T. t. orientalis* were said to be relatively large and

TABLE 5.—*Comparison of* Thunnus maccoyii *and the subspecies of* T. thynnus

[Mean values given in parentheses]

Character	*T. t. thynnus*	*T. t. orientalis*	*T. maccoyii*
Number of gill rakers	34–43 (38.9)	32–40 (35.9)	31–40 (33.7)
First ventrally directed parapophysis on vertebra number	8	8	9
9th vertebra: parapophysis height/least distance apart	1.2–29.6 (8.1)	1.1–12.7 (4.1)	0.8–3.2 (1.6)
10th vertebra: canal height/least width of processes	1.9–5.4 (3.5)	1.0–9.0 (4.1)	6.0–15.9 (11.3)
10th vertebra: canal height/canal width	1.5–3.2 (2.2)	1.4–4.8 (2.0)	0.9–1.7 (1.3)
Depth of anterior haemal canals	first increase, then decrease	first increase, then decrease	decrease
Shape of dorsal wall of body cavity in large specimens	wide bulge with no lateral concavity; deep, narrow lateral trough	narrow bulge with lateral concavity; wide lateral trough	wide bulge with no lateral concavity; deep, narrow lateral trough
Pectoral length as percent fork length (600–1,000 mm.)	17.0–21.7	16.8–20.8	20.2–23.0
Color of caudal keels	dark	dark	yellow

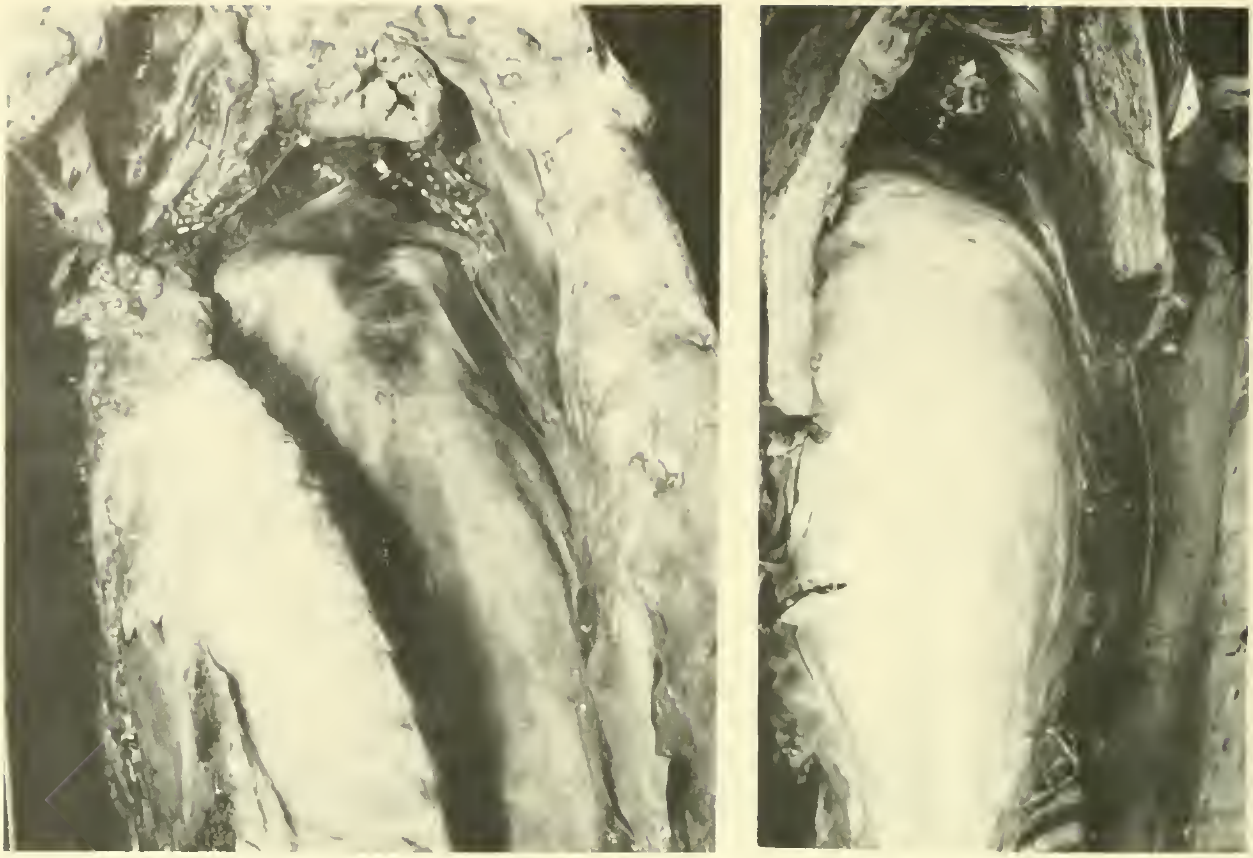


FIGURE 32.—Dorsal wall of body cavity of *Thunnus thynnus*. Ventral view with viscera removed and head end to the left. Left: *T. t. orientalis*, 1,450 mm. fork length, from California, showing the comparatively narrow anterior bulge with lateral concavity and wide lateral trough. Right: *T. t. thynnus*, 1,850 mm. fork length, from the western North Atlantic, showing the wide anterior bulge without a lateral concavity.

coarse compared with *T. maccoyii*. We could detect no differences.

The caecal mass is so variable in size that its dimensions cannot be used to differentiate populations.

The relative length of the lateral liver lobes of western Atlantic specimens encompasses the differences in lobe lengths suggested by Godsil and Holmberg.

The stomach length cannot logically be used as a specific character, since this is a highly distensible organ, the dimensions of which will vary under different physiological states.

Swimbladder dimensions vary with size, becoming larger with growth, as shown by Serventy (1956a) for *T. maccoyii* from Australia and by us for western Atlantic *T. t. thynnus* and eastern Pacific *T. t. orientalis*. Abe (1955) reported that the swimbladder was well developed in a 1,470-mm. specimen thought to be *T. maccoyii* from the eastern Indian Ocean. Kishinouye (1923) and Frade (1925) illustrated swimbladders for western Pacific and eastern Atlantic specimens, respectively, that are very similar to those of larger specimens from other regions, and Kishinouye noted that the swimbladder is short and very narrow in immature specimens of Japanese *T. thynnus orientalis*, but short and wide in adults.

Godsil and Holmberg described the posterior end of the kidney of *T. maccoyii* specimens as truncate. This condition was observed in several specimens of western Atlantic *T. t. thynnus*, which displayed all variations that have been described, but our specimens of *T. maccoyii* did not show this condition.

The branching of the ureter of *T. maccoyii* was said to differ in that the branching occurred well anterior in the kidney mass. We observed this condition in both *T. t. thynnus* and *T. t. orientalis*; in two of our three specimens of *T. maccoyii* the branching occurred near the end of the tail of the kidney.

In *T. maccoyii*, the dorsal aorta was reported to be usually conspicuously constricted behind the origin of the cutaneous arteries. We observed this condition in both *T. t. thynnus* and *T. t. orientalis*, but size did not decrease in our specimens of *T. maccoyii*.

The presence of a connecting branch between the two main branches of the coeliacomesenteric artery was said to distinguish *T. t. orientalis* and *T. maccoyii* from *T. t. thynnus;* however, Godsil and Holmberg (1950) did not find the branch in one Australian specimen and they were uncertain as to its presence in another. Furthermore, we observed this connection in several western Atlantic specimens.

The cutaneous artery in *T. maccoyii* was said to pass laterally most often between ribs 2 and 3 (rather than 3 and 4) and to divide usually between intermuscular bones 5 and 6 (rather than 4 and 5). Godsil and Byers (1944) recorded this condition as rare in *T. t. orientalis*, and Godsil and Holmberg (1950) noted the same for *T. t. thynnus.* In all our material, including *T. maccoyii*, the artery passed between ribs 3 and 4, and divided between intermuscular bones 4 and 5 (between 5 and 6 in one specimen of *T. t. thynnus*).

The place of attachment of the internal wing of the pelvic girdle was said to be different in each of the three forms (Godsil and Holmberg, 1950). We found the condition in all three similar to their descriptions of *T. maccoyii*.

THUNNUS MACCOYII (Castelnau, 1872)
SOUTHERN BLUEFIN TUNA

Thynnus maccoyii Castelnau, 1872: 104–105 (original description; Melbourne market).

Thunnus phillipsi Jordan and Evermann, 1926: 13 (original description; New Zealand), pl. 2, fig. 4.

Thunnus maccoyii, Jordan and Evermann, 1926: 13 (description). Serventy, 1941: 27–33 (description; Australia), fig. 5, pl. 2. Godsil and Holmberg, 1950 (comparison of Australian with New England and California specimens; anatomy). Mimura and Warashina, 1962. Iwai and Nakamura, 1964: 6, figs. 3E, F (olfactory rosettes). Iwai et al., 1965: 9 (synonymy), 33–34 (description), fig. 18. Nakamura, 1965: 18, figs. 3C, 5C, 7 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus obesus, Fraser-Brunner, 1950: 144 (*T. maccoyii* in synonymy).

Thunnus thynnus maccoyii, Serventy, 1956a (counts, distribution around Australia). Munro, 1958: 111 (Australia). Robins, 1963 (biology; Australia).

Thunnus thynnus subspecies, Serventy, 1956a: 13 (probably a separate subspecies in S. Africa).

Thunnus thynnus orientalis, Jones and Silas, 1960: 381–382 (Indian Ocean), fig. 8. Collette and Gibbs, 1963: 28. Jones and Silas, 1963: 1788–1790 (Indian Ocean). Talbot and Penrith, 1963: 630–636 (description, biology; S. Africa). Jones and Silas, 1964: 30–34 (Indian Ocean).

Types of Nominal Species

Thynnus maccoyii Castelnau, 1872. No type specimens. Bauchot and Blanc (1961: 377) reported that a type specimen was catalogued in the collections of the Museum National d'Histoire Naturelle, Paris, in 1877, as number 515, but that the specimen cannot be located. Original description based on several specimens, fresh and dried, from the Melbourne, Australia, market, the largest 23 inches (585 mm.) long. This description is inadequate, but the short pectoral (two-thirds of head) suggests one of the bluefin tunas or *T. tonggol*, and the locality rules out all except *T. maccoyii* as now recognized.

Thunnus phillipsi Jordan and Evermann, 1926. Type originally designated as "A photograph, No. 596, Mus. Calif. Acad. Sci. . . . of a specimen taken in the Bay of Islands, New Zealand." This photograph is of a pug-headed mounted specimen in the Dominion Museum, Wellington. The cast is 1,575 mm. FL. The pectoral fin is short (295 mm.), which makes *T. maccoyii* the only reasonable assignment for this nominal species, *T. tonggol* not being known to occur in New Zealand. According to J. Moreland (pers. comm.), the pug-headedness appears to be the result of the fish being stood on its head forcing the processes of the premaxillaries up over the frontals where they remained when the cast was made.

Characters

Pectoral fin short, not more than 80 percent of head length, 20–23 percent of fork length in specimens 650–1,450 mm. (overlapping *T. tonggol;* slightly longer than *T. thynnus*). Caudal keels yellow in most specimens; this color possibly lost in larger adults.

Gill rakers 31–40, more numerous than in any other species of *Thunnus* except *T. thynnus*.

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga*, *T. obesus*, and *T. thynnus*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Kidney with a very short "tail," reaching to the level of vertebra 8–12 (as in *T. thynnus*).

Cutaneous arteries originating at level of vertebra 4–5, passing laterally between ribs 2 and 3 or 3 and 4, and dividing between intermuscular bones 4 and 5 (as in *T. alalunga* and *T. thynnus*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. thynnus*). Post-cardinal vein absent (as in *T. alalunga* and *T. thynnus*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga*, *T. thynnus*, and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. thynnus* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids not known to fuse with parasphenoid as is the case in some *T. thynnus*. Subopercle relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. thynnus*); rarely, there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*). First closed haemal arch on vertebra 10 (as in *T. alalunga*, *T. thynnus*, and, rarely, all others except *T. tonggol*). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. alalunga*, *T. thynnus*, and *T. obesus*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga*, *T. thynnus*, and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga*, *T. thynnus*, and *T. obesus*).

Comparisons with *T. thynnus* are given in table 5.

Range

Thunnus maccoyii is apparently mainly restricted to the Southern Ocean, although it is impossible to evaluate many records. This species is best recognized at present by skeletal characters, although the yellow caudal keel is also diagnostic. We have examined skeletal material from Tasmanian waters reported by Godsil and Holmberg (1950); from western South Africa, reported by Talbot and Penrith (1963); additional specimens from the Sydney, Australia, market; from west of southern Australia; and from off the coast of Chile. The presence of *T. maccoyii* in the Pacific and Indian oceans off both sides of southern Australia and off Chile, and in the Atlantic off South Africa is thus definitely established. The geographic distribution summarized by Robins (1963) included waters north of New Zealand and areas off western Australia north almost to the Indonesian Islands. These records are probably correct, but need confirmation through osteological studies. Southeastern Pacific catches are reported by Japanese expeditions (Japan Fishery Agency, 1964). If these unconfirmed records are accepted, it seems likely that *T. maccoyii* will be found throughout the Southern Ocean south of 30° S.

THUNNUS THYNNUS (Linnaeus, 1758)
BLUEFIN TUNA

The synonymy of each of the two subspecies is presented separately. The diagnosis of the species, discussion of nominal species and subspecies, and summary of the range consider both subspecies.

THUNNUS THYNNUS THYNNUS (Linnaeus, 1758)
ATLANTIC BLUEFIN TUNA

Scomber pinnulis octo vel novem in extremo dorso ex sulco ad pinnas ventrales Artedi, 1738a: 31 (description) and 1738b: 141–142 (references to Aristotle, Ovid, Pliny, etc.).

Scomber thynnus Linnaeus, 1758: 297–298 (original description; based on Artedi, 1738). Bonnaterre, 1788: 139, pl. 58, fig. 228. Gmelin, 1789: 1330–1331 (description, synonymy). Lacépède, 1800: 598, 605–632 (description, synonymy). Risso, 1810: 163 (Nice).

Thynnus thynnus, Cuvier, 1817: 313 (Mediterranean). Günther, 1860: 362–363 (synonymy, description; Atlantic and Mediterranean).

Thynnus mediterraneus Risso, 1826: 414–415 (substitute name for *Scomber thynnus* Linnaeus, 1758; Nice).

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831: 42–71 (substitution of new name for *Scomber thynnus* Linnaeus, 1758), pl. 210.

Thunnus vulgaris, South, 1845: 620–621 (description, natural history).

Thynnus secundo-dorsalis Storer, 1967: 65–67 (original description; Massachusetts Bay), pl. 12, fig. 4.

Orcynus thynnus, Poey, 1875: 144–145. Lütken, 1880: 460–464, 595–596 (in part; development). Buen, 1925 (migrations, biology; E. Atlantic).

Orcynus secondidorsalis, Poey, 1875: 145 (Cuba).

Albacora thynnus, Jordan, 1888. Dresslar and Fesler, 1889: 439–440 (synonymy in part), pl. 7.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description, synonymy in part; a single worldwide species of bluefin). Meek and Hildebrand, 1923: 314–315 (description, synonymy in part). Jordan and Evermann, 1926: 10 (synonymy; Europe). Barnard, 1927: 798–799 (S. Africa). Buen, 1930: 49 (synonymy), fig. 7. Frade, 1931b (biometrics; Portugal). Frade, 1931c (meristics; E. Atlantic). Crane, 1936 (description; Gulf of Maine). Fowler, 1936: 619–620 (synonymy, description). Tortonese, 1939: 324 (Yokohama). Bellón and Bardán de Bellón, 1949: 8–11 (Canary Is.). Smith, 1949, 1953: 298 (S. Africa), pl. 66, fig. 831. Godsil and Holmberg, 1950 (anatomy; New England). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part), fig. 4. Rivas, 1951: 217–219 (description, synonymy). Ginsburg, 1953: 1 (the name *thynnus* restricted to the E. Atlantic population of bluefin). Morice, 1953: 67–68, figs. 1, 2 (liver; E. Atlantic). Bellón, 1954 (description, relationships, biology, anatomy, distribution). Mather and Day, 1954: 181 (W. Atlantic). Rivas, 1954b: 302–322 (spawning in straits of Florida), figs. 1–3. Rivas, 1955 (comparison between Gulf of Maine and Florida specimens). de Sylva, 1955: 33–40 (osteology, relationships), fig. 55 (neurocranium). Bullis and Mather, 1956 (key to Caribbean species of *Thunnus*). Robins, 1957 (counts on dorsal and anal fins, gill rakers; one species of bluefin in the Atlantic). Mather and Schuck, 1960 (growth; NW. Atlantic). Frade and Vilela, 1962: 17–58 (morphology, biology; E. Atlantic). Tiews, 1963 (biology; Atlantic.)

Thunnus secundodorsalis, Jordan and Evermann, 1926: 12 (description). Jordan et al., 1930: 260. Ginsburg, 1953: 1–3 (W. Atlantic; summary of meristics from various authors).

Thunnus thynnus thynnus, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of Europe). Talbot and Penrith, 1963: 633–640 (description, biology; S. Africa).

Thunnus thynnus coretta, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of America).

Misidentification

Thynnus brachypterus Cuvier (1829) was based on illustrations by Rondelet (1554) and Duhamel du Monceau (1769). Collette (1966) has indicated that this name is a synonym of *Sarda sarda* (Bloch). Although Cuvier (*in* Cuvier and Valenciennes, 1831) based his later description of *T. brachypterus* on specimens, four of which are *T. thynnus* and one *Euthynnus alletteratus*, this can not be regarded as the original description, and these specimens are not types.

Types of Nominal Species

Scomber thynnus Linnaeus, 1758. No type specimens. Original description not diagnostic, but based on Artedi (1738a, p. 31), who stated: "Longitude 7 pedum circiter." This could only refer to the bluefin tuna.

Thynnus mediterraneus Risso, 1826. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus secundodorsalis Storer, 1867. No type specimens. Original description based on two specimens, 8 feet, 6 inches (1,590 mm.) and 9 feet, 3 inches (1,820 mm.) total length. The pectorals "about one seventh of length of fish," the size and the locality (Mass.) unquestionably assign this nominal species to the synonymy of *Thunnus thynnus thynnus*.

THUNNUS THYNNUS ORIENTALIS

(Temminck and Schlegel, 1844)

PACIFIC BLUEFIN TUNA

Thynnus orientalis Temminck and Schlegel, 1844: 94–95 (original description; Japan). Günther, 1860: 362 (in footnote as dubious species).

Orcynus schlegelii Steindachner *in* Steindachner and Döderlein, 1884: 10–11 (original description; Tokyo), pl. 3, fig. 1.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description and synonymy in part). Jordan et al., 1913: 121 (Japan). Walford, 1937: 7–13 (description; Pacific specimens; possibility of a single worldwide species of bluefin), color pl. 34.

Brock, 1938 (Washington). Godsil and Byers, 1944: 88–102 (anatomy; E. Pacific), figs. 48–58. Tinker, 1944: 151 (Hawaii), pl. 1, fig. 8. Brock, 1949: 276 (key to Hawaiian tunas). Fraser-Brunner, 1950: 142–143 (synonymy in part), fig. 4. Godsil and Holmberg, 1950 (anatomy; California). June, 1952a (Hawaii). Buen, 1953 (Chile; but might be *T. maccoyii*). Iwai and Nakamura, 1964: 6, figs. 3C, D (olfactory rosettes). Iwai et al., 1965: 3, 6–8 (synonymy), 31–33 (description), fig. 16. Nakamura, 1965: 17–18, figs. 3B, 5B, 6 (osteology). Nakamura and Warashina, 1965: 9–10 (E. Indian and SE. Pacific oceans). Nakamura and Kikawa, 1966 (infracentral grooves).

Orcynus thynnus, Kitahara, 1897: 1 (description; Japan), pl. 1, fig. 1.

Thunnus schlegelii, Jordan and Snyder, 1900: 352 (Tokyo). Jordan and Snyder, 1901: 64 (Yokohama).

Thunnus orientalis, Kishinouye, 1915: 17 (description, anatomy; Japan), pl. 1, fig. 9. Kishinouye, 1923: 437–442 (anatomy; Japan), figs. 3, 21, 43, 44, 50. Jordan and Hubbs, 1925: 216–217 (Japan). Jordan and Evermann, 1926: 14 (description). Tinker, 1944: 157–158 (Hawaii). Brock, 1949: 276 (key to Hawaiian tunas). Gosline and Brock, 1960: 259 (description; Hawaii), 336 (synonymy), fig. 257h. Yamanaka et al., 1963 (biology; Japan).

Thunnus saliens Jordan and Evermann, 1926: 10–11 (original description; California), pls. 1–2, figs. 1–3. Jordan et al., 1930: 259. Ginsburg, 1953: 3 (*saliens* recognized as American Pacific species of bluefin). Neave, 1959 (N. end Vancouver Is.). Bell, 1963 (biology; E. Pacific).

Thunnus thynnus orientalis, Serventy, 1956a: 11–13 (the subspecies found along Asiatic coast of N. Pacific).

Thunnus thynnus saliens, Serventy, 1956a: 11–13 (the subspecies found along Pacific coast of N. America). Buen, 1958: 24–25 (Chile; but might be *T. maccoyii*).

Types of Nominal Species

Thynnus orientalis Temminck and Schlegel, 1844. Holotype RMNH 794, 450 mm. fork length, a mounted specimen from Japan with a pectoral fin 18.4 percent of fork length.

Orcynus schlegelii Steindachner, 1884. Holotype (not seen by us) presumably in Vienna Museum, 360 mm. fork length. The pectoral of barely more than half the head length and the locality (Japan) enable referral of this nominal species to the synonymy of *T. thynnus orientalis* (Temminck and Schlegel, 1844).

Thunnus saliens Jordan and Evermann, 1926. Type originally designated as "No. 595, Mus. Calif. Acad. Sci., a photograph of a specimen weighing 157½ pounds taken . . . off Catalina, California." The photograph is clearly of a tuna with short pectoral fins; Jordan and Evermann (1926) recorded the fin length as 5½ (p. 9) or 5 (p. 10) in (standard) length, or about 20 percent. The locality allows referral to the synonymy of *T. thynnus orientalis*.

Characters

Pectoral fin short, not more than 80 percent of head length, less than 23 percent of fork length, slightly shorter than in *T. maccoyii* at a given size (fig. 33), overlapped by *T. tonggol*.

Gill rakers 34–43 in *T. t. thynnus*, 32–40 in *T. t. orientalis*, more numerous than in any other species of *Thunnus* except *T. maccoyii*.

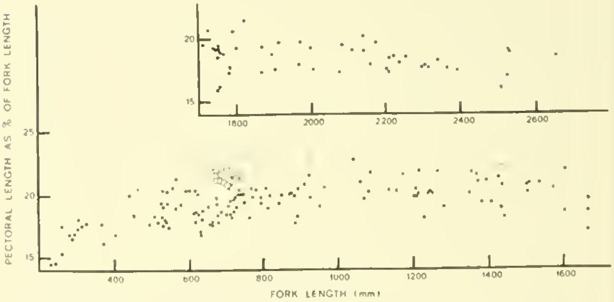


FIGURE 33.—Relative length of pectoral fin in *Thunnus thynnus* (dots) and *T. maccoyii* (open circles).

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga*, *T. obesus*, and *T. maccoyii*). Spleen located on right side, stomach on left (as in all except *T. alalunga*). Kidney with a very short tail, reaching to level of vertebra 8–11 (as in *T. maccoyii*).

Cutaneous arteries originating at level of vertebra 3–6 (usually 4 or 5), passing laterally between ribs 3 and 4 (occasionally 2 and 3) and dividing between intermuscular bones 4 and 5 or 5 and 6 (as in *T. alalunga* and *T. maccoyii*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. maccoyii*). Post-cardinal vein absent (as in *T. alalunga* and *T. maccoyii*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga*, *T. maccoyii*, and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. maccoyii* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids fused to parasphenoid in some larger specimens. Subopercle (see fig. 9) relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. maccoyii*); rarely there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 8. First closed haemal arch usually on vertebra 10 (as in *T. alalunga* and *T. maccoyii*), sometimes on 11 (as in the other five species). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. maccoyii* and *T. obesus*). All haemal postzygapophyses short, less than half the centrum length (as in *T. maccoyii* and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga*, *T. maccoyii*, and *T. obesus*).

Comparisons with *T. maccoyii* are given in table 5.

Range

T. thynnus thynnus has been found in the western Atlantic from Hamilton Inlet, Labrador (La Monte, 1946: 22), and Newfoundland, south along the Atlantic coast of the United States into the Gulf of Mexico and Caribbean Sea (Wathne, 1959). It is known off Venezuela (Fernandez-Yepez and Santaella, 1956), and south to northeastern Brazil. In the eastern Atlantic, *T. t. thynnus* is found from the Lofoten Islands of Norway (about 70° N.), south along the coast of Europe and north Africa, south to the Canary Islands. Records from near Cape Verde Islands, Angola, and Republic of South Africa have been questioned (Tiews, 1963), but gill-raker counts given by Talbot and Penrith (1963) for large specimens caught from January to March suggest convincingly that *T. t. thynnus* does occur west of the Cape Peninsula of South Africa, and we have examined one specimen from there.

Tag returns have shown that there is at least some interchange between eastern and western North Atlantic *T. t. thynnus*. Mather (1960) reported two specimens tagged off Martha's Vineyard, Mass., and recaptured in the Bay of Biscay 2 to 5 years later. Two large specimens tagged off Cat Cay, Bahamas, were recaptured off Bergen, Norway, a distance of over 4,000 miles, after 118 and 119 days at large (Mather, 1962).

T. thynnus orientalis has been reported in the eastern north Pacific from the Shelikof Straits, north of Kodiak Island, in the Gulf of Alaska (Radovich, 1961), off Vancouver Island (Neave, 1959), off Willapa Bay and the mouth of the Columbia River (Brock, 1938), regularly off southern California and the length of Baja Calif. (Bell, 1963). In the western north Pacific, *T. t. orientalis* is known from the island of Sakhalin in the southern Okhotsk Sea, southward on both sides of Japan, to the northern Philippines; eastward from Japan between about 30°–40° N. to about 160° W.; and eastward between about 5°–10° N. from about 135°–175° E. (Yamanaka et al., 1963). It is taken occasionally in Hawaiian waters (Jordan and Jordan, 1922; Fowler, 1928; June, 1952a).

The contention that both eastern and western north Pacific *T. thynnus* constitute a single subspecies is supported by the recapture off Japan of at least three specimens that had been tagged 2 to 5 years previously near Guadalupe Island, Mexico (Orange and Fink, 1963; Anonymous, 1964).

Thunnus thynnus has been recorded from the Galapagos area (Snodgrass and Heller, 1905; Herre, 1936), but there is no supporting evidence which would eliminate *T. maccoyii* or any other species from consideration.

Nakamura and Warashina (1965) reported *T. thynnus orientalis* (as *T. thynnus*) from two areas previously not verified. Two specimens, 2,657 mm. and 2,200 mm., were taken in the Indian Ocean off western Australia at 28°24′ S., 105°56′ E. and 27°43′ S., 102°25′ E., respectively. Another, 2,206 mm., was captured in the southeastern Pacific at about 37°11′ S., 114°41′ W. Specimens from Chile had previously been reported by Buen (1953, 1958), as *T. thynnus saliens*. These are areas from which *T. maccoyii* is known. Nakamura and Warashina gave measurements of one specimen from each locality. Converting their figures for pectoral length into percent of fork length (their "total length") gives 18.6 and 17.5 percent, falling below our data for smaller *T. maccoyii* and agreeing well with *T.*

thynnus orientalis (table 5). All three, however, are much larger than the largest reliably identified *T. maccoyii* (1,748 mm.; Iwai and Nakamura, 1964b: 2). It is entirely possible that the two best external diagnostic characters—color of caudal keel and length of pectoral fin—may no longer be distinct at large sizes. At the present time only examination of vertebral characters can offer assurance of their identity.

We examined the skull and vertebral column of the specimen from 37°11′ S., 114°41′ W. The skull (290 mm.) is larger than any we have examined of *T. maccoyii* and has the alisphenoids fused to the parasphenoids, a condition we have found only in large specimens of *T. thynnus*. The first ventrally directed parapophyses are on the eighth vertebra and the first closed haemal arch is on the tenth vertebra as in *T. thynnus*. Three other vertebral characters useful in distinguishing *T. thynnus* from *T. maccoyii* have the following values: 9th vertebra: parapophysis height divided by least distance apart —4.2; 10th vertebra: canal height divided by least width of processes—2.9; and 10th vertebra: canal height divided by canal width—1.8. The first and third are higher and the second is well below the range we have found for *T. maccoyii*, and all agree well with our data for *T. t. orientalis* (table 5). Unfortunately, skeletons of the suspect Indian Ocean specimens are not available, but specimens from this region, observed by us in the Yaizu market, appeared to have the dorsal bulge of the body cavity as in *T. thynnus*.

THUNNUS TONGGOL (Bleeker, 1851)
LONGTAIL TUNA

Thynnus tonggol Bleeker, 1851: 356–357 (original description; Batavia Sea). Günther, 1860: 364.

Thunnus rarus Kishinouye, 1915: 28 (original description; Tokyo market), pl. 1, fig. 13.

Neothunnus rarus, Kishinouye, 1923: 448–450 (anatomy), figs. 24–48, 64. Herre, 1940: 39 (Malaya). Nichols and La Monte, 1941: 32 (synonymy in part).

Kishinoella rara, Jordan and Hubbs, 1925: 219 (placed in the new genus *Kishinoella*). Jordan and Evermann, 1926: 26 (description). Herre, 1945: 148 (Zamboanga, Philippines).

Neothunnus tonggol, Jordan and Evermann, 1926: 22.

Thunnus nicolsoni Whitley, 1936: 30–31 (original description; Queensland), fig. 2.

Thunnus tonggol, Tortonese, 1939: 326 (Java Sea). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 145–146 (synonymy), fig. 8. de Beaufort, 1951: 225–226 (synonymy; description; Bleeker's types checked). Iwai and Nakamura, 1964: 6, fig. 31 (olfactory rosettes). Jones and Silas, 1964: 38–40 (Indian Ocean). Iwai et al., 1965: 16–17 (synonymy), 39–40 (description), fig. 23. Nakamura, 1965: 24, figs. 3G, 12, 13A (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Kishinoella tonggol, Serventy, 1941: 33–38 (description; Australia), figs. 6–9, pl. 2. Serventy, 1942 (description, anatomy, synonymy; Australia), fig. 1, pls. 3–5. Serventy, 1956b (counts, distribution; Australia). Munro, 1958: 111 (Australia.) Jones and Silas, 1960: 384–385 (west coast of India), fig. 11. Ranade, 1961 (description; Arabian Sea). Jones, 1963 (biology; Indian Ocean). Jones and Silas, 1963: 1792–1793 (Indian Ocean).

Misidentifications

Munro (1957) reported a specimen of tuna as *Parathunnus mebachi* from southern Queensland. Rivas (1961) considered this specimen to be the same as his *T. argentivittatus*, but as we have shown under the account of *T. albacares*, Rivas' account and that of Schaefer and Walford (1950) is based on a specimen of *T. tonggol*. Judging from the low number of gill rakers (7+16=23), pectoral length, and distance from snout to second dorsal origin reported by Munro (1957), his specimen was also *T. tonggol*. His later account (Munro, 1958) confirms this opinion. Serventy (1942, 1956b), Fraser-Brunner (1950), and others have considered *Kishinoella zacalles* Jordan and Evermann (1926) as close to or a synonym of *T. tonggol*, but *zacalles* is a synonym of *T. albacares*, as we show under the account of that species.

Types of Nominal Species

Thynnus tonggol Bleeker, 1851. No type specimens known to us. The designation of a neotype by Boeseman (1964) was not in accordance with the International Code of Zoological Nomenclature (1964, Article 75), which states, among other things, that a neotype is to be designated only in connection with revisionary work, and that the designator of a neotype must give his reasons for believing all original type material to be lost or destroyed and the steps that have been taken to trace it. Since designation of a neotype would solve no nomenclatorial problems, and since we have not exhaustively sought type material, we do not deem it necessary or proper to take this action ourselves.

Bleeker's original description was based on a single specimen, 650 mm. long, from "Batavia, in mari," with a pectoral fin shorter than the head and no swimbladder. The description obviously applies to the species for which the name is now used.

Thunnus rarus Kishinouye, 1915. No type specimens. Original description based on a single specimen, 28.8 inches (ca. 730 mm.) long, from Nagasaki. The gill-raker count of 6+17, short pectoral fins (no measurements given), and lack of swimbladder show this nominal species to be a synonym of *T. tonggol*.

Thunnus nicolsoni Whitley, 1936. Holotype Australian Museum IA. 6553, a 189 mm. head of a specimen originally 30 inches (762 mm.) total length caught between Lindeman and Maher Islands, Cumberland Group, North Queensland, Australia. The gill raker count of 6+16 and pectoral shorter than head establish this as a synonym of *T. tonggol*.

Characters

Pectoral fin (see fig. 26) varying in length from medium (22–31 percent of fork length) in specimens less than 600 mm. to short (16–22 percent) in those over 600 mm. (the latter resembling only *T. thynnus* and *T. maccoyii*). Tail region comparatively long, longest in large specimens; distance from snout to second dorsal origin 49–55 percent of fork length, decreasing with size (consistently lower than in any other *Thunnus* species).

Gill rakers 19–26 (rarely to 28), fewer than in any other *Thunnus* species except *T. atlanticus*.

Liver without striations on ventral surface, its right lobe long and narrow, without vascular cones on its dorsal side (as in *T. albacares* and *T. atlanticus*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Kidney with a bulky anterior mass and a long, narrow tail, reaching vertebra 15–17.

Swimbladder absent or rudimentary.

Cutaneous arteries originating at the level of vertebra 7–8, passing laterally between ribs 4 and 5 or 5 and 6, dividing between intermuscular bones 6 and 7 (as in *T. albacares*, *T. obesus*, and *T. atlanticus*). A single row of arterioles and venules arising from each cutaneous branch (as in *T. alalunga*, *T. albacares*, and *T. atlanticus*), but arising from the lateral side of each vessel (as in *T. albacares* and *T. atlanticus*).

Post-cardinal vein present (as in *T. albacares*, *T. atlanticus*, and *T. obesus*).

Posterior parasphenoid margin not angulate (similar to *T. albacares* and *T. atlanticus*).

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis usually on vertebra 10. First closed haemal arch usually on vertebra 11 (as in *T. atlanticus*, *T. albacares*, *T. obesus*, occasionally *T. thynnus*) or 12. Anterior haemal prezygapophyses arising well ventrad on haemal spines (as in *T. albacares* and *T. atlanticus*). Haemal postzygapophyses long, the longest about equal to or longer than centrum length (as in *T. atlanticus*, slightly longer than in *T. albacares*). Anteriormost ventrolateral foramina large, more than three times as wide as haemal spine (as in *T. albacares* and *T. atlanticus*).

Nominal Species

There appear to be only two synonyms of *T. tonggol: Thunnus rarus* Kishinouye from Japan and *T. nicolsoni* Whitley from Queensland. Rivas (1961) placed *T. nicolsoni* in the synonymy of *T. albacares* but the gill raker count of 6+16=22 alone (Whitley, 1936) is enough to show that this is incorrect.

Range

T. tonggol is limited to the Indo-West Pacific. It is found from the western and southern coasts of Kyushyu and the southwestern part of the Japan Sea (Kishinouye, 1923, p. 449), south through the Batavia Sea (Bleeker, 1851, p. 356) to New Guinea, New Britain, and the entire north coast of Australia (Serventy, 1956b). On the Australian east coast, it is reported at least as far south as Twofold Bay, New South Wales; on the west coast it reaches at least to Cockburn Sound in the Freemantle area. Its range in the Indian Ocean (Jones, 1963) includes the Indo-Australian Archipelago, Andaman Islands, both coasts of India, southern Arabia, the Somalia coast, and the Red Sea, but it was not reported from East African waters by Williams (1964) or Merrett and Thorp (1966).

Gill-raker counts indicate differences between populations in the western Indian Ocean, with a modal number of 26, and those in the eastern Indian Ocean and western Pacific, with a mode of 23. More data are necessary to corroborate this.

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APPENDIX

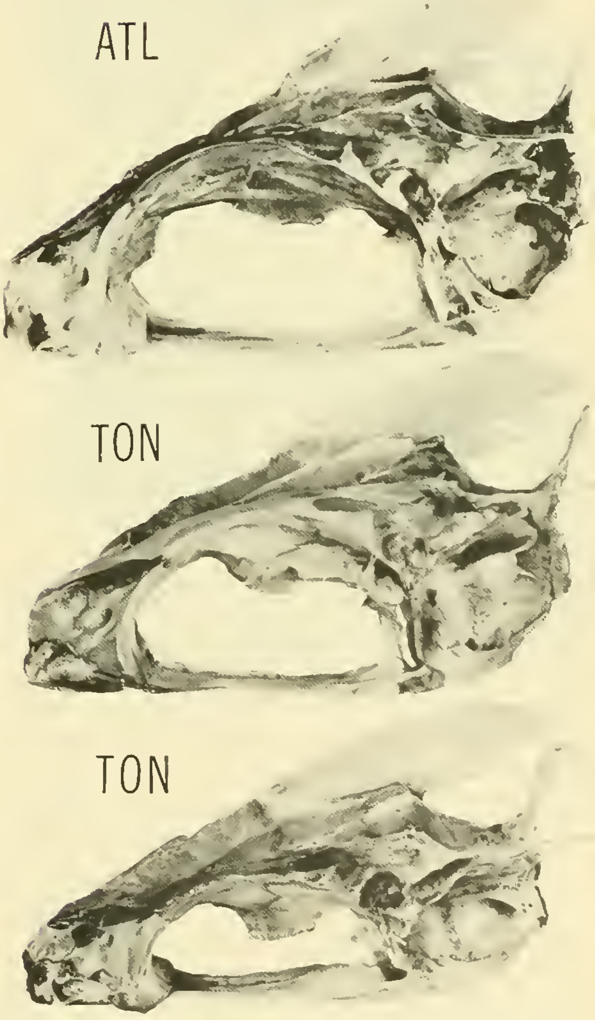

FIGURE A-1.—Lateral view of skulls of *Thunnus* species. (top) *T. atlanticus*, skull length 88 mm.; (middle) *T. tonggol*, 56 mm.; (bottom) *T. tonggol*, 122 mm.

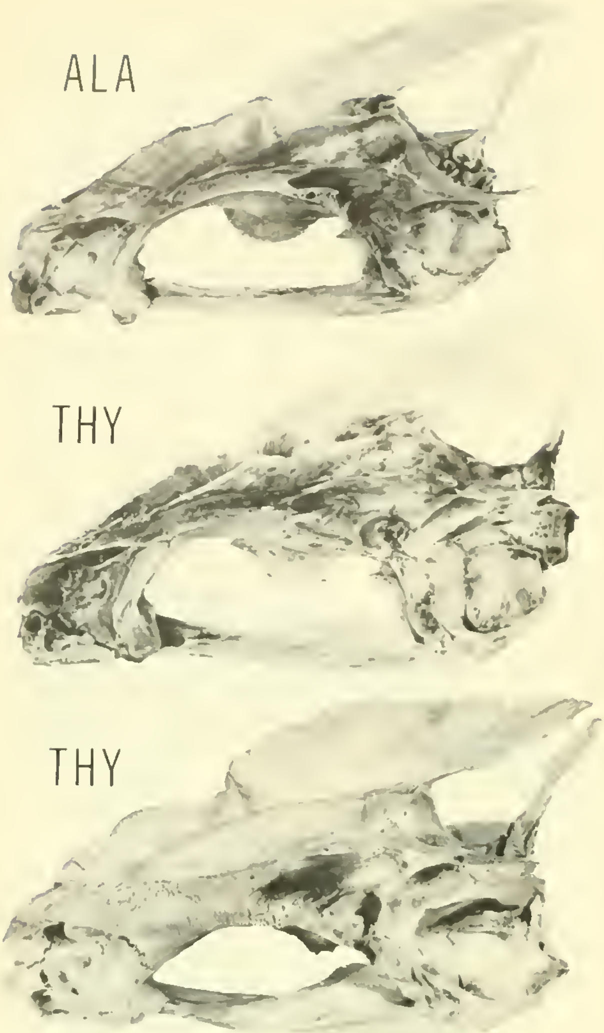

Figure A-2.—Lateral view of skulls of *Thunnus* species. (top) *T. alalunga*, skull length 151 mm.; (middle) *T. thynnus*, 103 mm.; (bottom) *T. thynnus*, 335 mm.

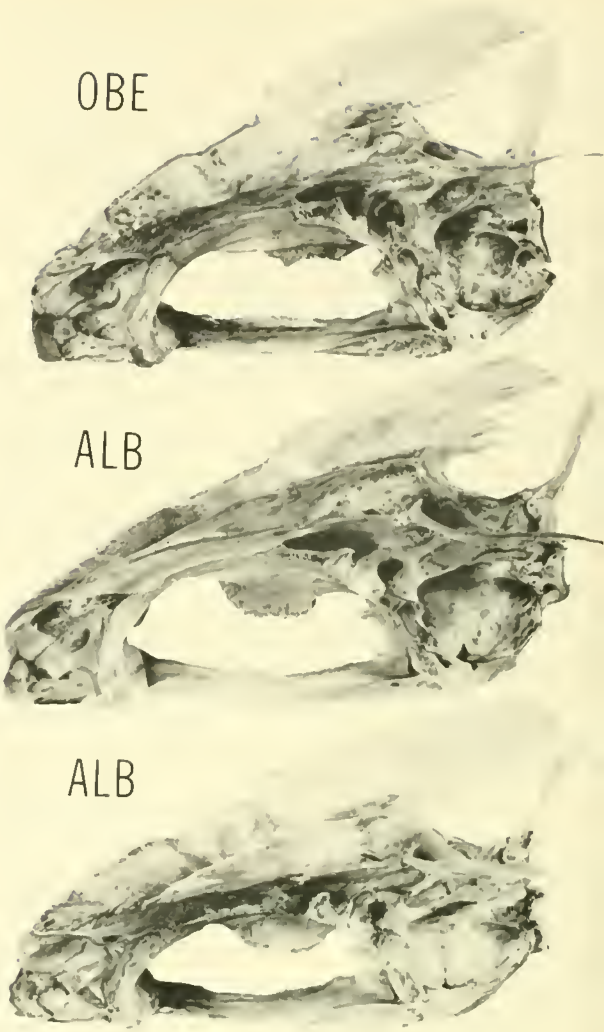

Figure A-3.—Lateral view of skulls of *Thunnus* species. (top) *T. obesus*, skull length 200 mm.; (middle) *T. albacares*, 113 mm.; (bottom) *T. albacares*, 164 mm.

INFLUENCE OF ROCKY REACH DAM AND THE TEMPERATURE OF THE OKANOGAN RIVER ON THE UPSTREAM MIGRATION OF SOCKEYE SALMON

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ABSTRACT

Tagging experiments show that Rocky Reach Dam, constructed on the Columbia River 7 miles above Wenatchee, Wash., in 1957–61, has not appreciably increased the time required for adult sockeye salmon (*Oncorhynchus nerka*) to migrate to Zosel Dam on the Okanogan River (a tributary to the Columbia River above Rocky Reach Dam). Water temperature of the Okanogan River is, however, a major cause of delay. Above 70° F., rising or stable Okanogan River temperatures block the entry of the fish from the Columbia River into the Okanogan River; falling temperatures allow the migration to resume. Below 70° F., migration is not blocked by rising or stable temperatures. Delay may reduce survival because it increases the exposure of the sockeye salmon to other factors that affect them adversely.

INTRODUCTION

If Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) are to reproduce successfully, sufficient adults in spawning condition must reach the spawning grounds. Consequences can be serious if the migrants are delayed en route. Thompson (1945) showed, for example, that of the tagged sockeye salmon (*Oncorhynchus nerka*) that had been delayed longer than 12 days at the Hell's Gate rock slide on the Fraser River, British Columbia, in 1941, practically none reached their spawning grounds. He also suggested that lesser delays reduced the reproductive capacity of the fish.

Although they are equipped with facilities for passing fish, hydroelectric dams on the migration routes constitute another type of barrier which can delay adults en route to their upstream spawning grounds. To assess and find ways to minimize the effects of these dams as they are built on the Columbia River is a most important aim of the agencies concerned with the salmon and steelhead resources of the stream. One facet of this work is to detect and minimize any delay of the adults as they migrate upstream. The time required for adults to locate and ascend fish ladders is sometimes reduced, for example, by altering the spill pattern to improve attraction to the ladders or even by modifying the ladders themselves.

In this paper we show that Rocky Reach Dam, constructed on the Columbia River, 7 miles above Wenatchee, Wash., in 1957–61, has not appreciably increased the time required for sockeye salmon to migrate from Rock Island Dam (below Rocky Reach Dam) to Zosel Dam on the Okanogan River, a tributary to the Columbia River above Rocky Reach Dam (fig. 1). We also illustrate how the temperature of the Okanogan River periodically blocks the upstream migration of the sockeye salmon at the confluence of the Okanogan and Columbia Rivers.

This study originated as part of a broad program to assess the effects of Rocky Reach Dam on the fish and wildlife resources of the upper Columbia River. The program was developed by representatives of interested State and Federal agencies and financed by Public Utility District Number 1 of Chelan

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Note.—Approved for publication April 28, 1966.

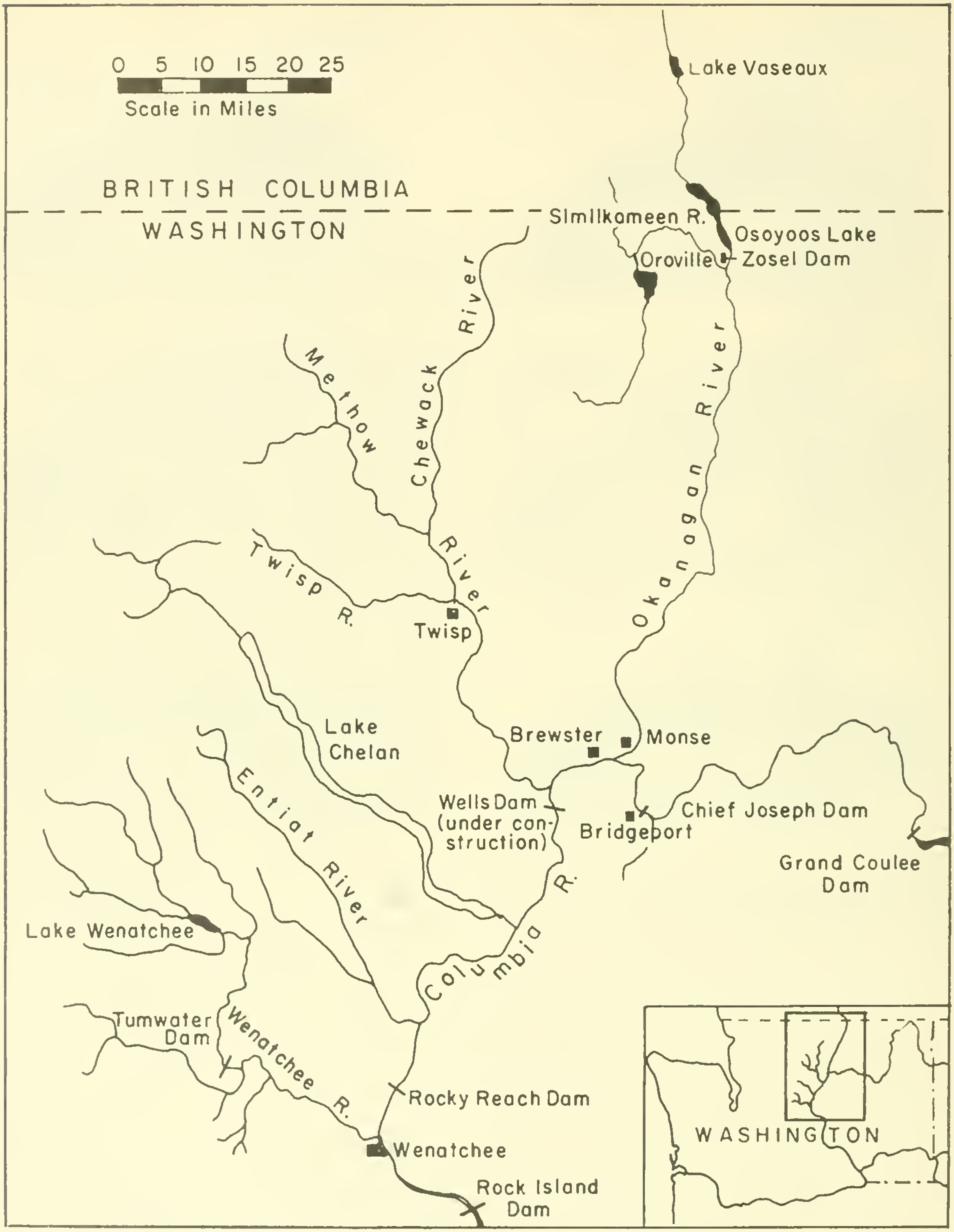
0 5 10 15 20 25
Scale in Miles
BRITISH COLUMBIA
WASHINGTON
Lake Vaseaux
Similkameen R.
Osoyoos Lake
Oroville
Zosel Dam
Chewack River
Methow
Okanogan River
Twisp R.
River
Twisp
Lake Chelan
Brewster
Monse
Wells Dam (under construction)
Bridgeport
Chief Joseph Dam
Grand Coulee Dam
Entiat River
Columbia R.
Lake Wenatchee
Tumwater Dam
Wenatchee R.
Rocky Reach Dam
Wenatchee
Rock Island Dam
WASHINGTON

FIGURE 1.—The Columbia River and the locations important to the present study.

County, the builders of Rocky Reach Dam, in accordance with the terms of Federal Power Commission license number 2145. Biologists of the Bureau of Commercial Fisheries were designated to study possible delay because of their experience with a similar investigation at Rock Island Dam in 1953–56 (French and Wahle, 1966).

The study underwent a major expansion as it proceeded. Originally, the sole aim was to measure delay, if any, caused to upstream-migrating adult salmonids by Rocky Reach Dam. This aim was to be accomplished by comparing the time required for tagged sockeye salmon to migrate from the forebay (reservoir) of Rock Island Dam to Zosel Dam, before (1957) and after (1962 and 1963) the completion of Rocky Reach Dam. If minimal influence by other factors were assumed, any major change in travel time could be attributed to the new structure.

French and Wahle (1960) summarized the "predam" work (performed before the dam was built). Because too few tagged fish were observed at Zosel Dam in 1957, they estimated the travel time (10.7 days) from tagged sockeye salmon that had been released in the Rock Island Dam forebay and later observed at Zosel Dam during the earlier (1953–56) study.

The tagging results in the first "postdam" year (1962) had a profound impact on our investigation. Sockeye salmon migrating through the study area were noticeably delayed—apparently by high water temperatures of the Okanogan River. If a temperature block were shown to exist, the assumption of minimal influence by factors other than Rocky Reach Dam would have been invalidated and the straightforward comparison of "predam" and "postdam" travel times as a measure of delay ruled out—unless the influence of the various factors could be examined separately. It was necessary, therefore, to confirm the existence of the temperature block, to reexamine the estimated "predam" travel time, and finally to evaluate Okanogan River temperatures as well as Rocky Reach Dam as sources of delay to sockeye salmon in their upstream migration. These expanded objectives greatly increased the complexity of the "postdam" phase of the study.

METHODS AND MATERIALS

The experimental procedure was as follows: (1) determine, both before and after the completion of Rocky Reach Dam, the time required for tagged sockeye salmon to migrate from the Rock Island forebay to Zosel Dam; (2) determine the time required for tagged sockeye salmon to migrate from the Rock Island forebay to Rocky Reach Dam; (3) examine the variability in passage time in relation to Rocky Reach Dam and the flows and temperatures of the Okanogan and Columbia Rivers.

Tagging experiments provided the answers to items (1) and (2). For item (3), these same tagging data were supplemented by counts of sockeye salmon made at Rock Island and Zosel Dams in years when there was no tagging.

SOCKEYE SALMON AS THE STUDY SPECIES

Observations were confined to sockeye, the only salmon that can be intercepted in significant numbers above Rocky Reach Dam while still actively migrating to the spawning grounds.

Most sockeye salmon that pass Rock Island Dam are bound for spawning areas in the Wenatchee and Okanogan River systems. Those that pass Rocky Reach Dam are, on the other hand, mostly Okanogan-bound fish, because the Wenatchee population leaves the main Columbia River below Rocky Reach Dam. After sockeye salmon pass Rocky Reach Dam, they move to the mouth of the Okanogan River near Brewster, Wash., and continue up the Okanogan into Lake Osoyoos, where they remain until they migrate to the spawning grounds, 10 to 15 miles above the lake, in late September. We have assumed that the Okanogan and Wenatchee populations pass Rock Island Dam simultaneously. The close similarity in the shapes of the graphs of sockeye salmon counts for Rock Island and Rocky Reach Dams (examples of which are shown in figure 10, in conjunction with other data) suggests that this assumption is reasonable.

TAGGING

Sockeye salmon were tagged at Rock Island Dam in 1953–57, before Rocky Reach Dam was constructed, and in 1962 and 1963, after construction. The numbers of tagged sockeye salmon that were later observed at Zosel Dam in 1953, 1954, 1962, and 1963 are presented in table 1. The effort to observe tagged sockeye salmon at Zosel Dam was so variable and so ineffective in 1955–57 (for reasons given later) that data for these years are not included.

The tagging procedure was the same each year. Tagging was started when the daily count reached about one thousand fish and continued until it dropped to about one thousand near the end of the

TABLE 1.—*Number of sockeye salmon tagged at Rock Island Dam and observed at Zosel Dam in 1953, 1954, 1962 and 1963*

Year	Tagged at Rock Island Dam	Observed at Zosel Dam
	Number	*Number*
1953	710	334
1954	1, 234	215
1962	1, 009	89
1963	730	193

run. In 1954 and 1963, tagging was continued for periods of 2 to 4 consecutive days, separated by intervening 3 to 4 day periods of no tagging. Tagging was all at the end of the run in 1953 and was confined to the middle portion of the small run in 1962.

The method of tagging was standard for these studies. Fish were trapped at Rock Island Dam in either the fishway or forebay (figs. 2 and 3), transported by tank truck to the release sites, tagged, and released. Tagging time seldom exceeded 30 seconds per fish.

Several types and colors of tags were used. Petersen plastic disks were used alone in 1962 and 1963, but were used in combination with plastic bars and vinyl streamers in 1953 and 1954. Nickel pins, inserted through the body just below the dorsal fin, provided the attachment. Tags were always applied in pairs, so that the same color and type of tag showed on both sides of the fish.

STATIONS FOR COUNTING SOCKEYE SALMON AND OBSERVING TAGS

Zosel Dam, which lies on the Okanogan River at Oroville, Wash., 1 mile below Lake Osoyoos, is the principal upstream location for the observation of tagged fish. The dam, which forms a sawmill pond, is provided with two fishways, each with a trap at its exit for the capture of upstream-migrating fish. Sockeye salmon were counted at Zosel Dam in 1935–37, 1944, 1952–57, 1962, and 1963. Since the dam was modified in 1948, however, fish have been able to pass upstream at certain water levels without using the fishways. When stream flow exceeds the

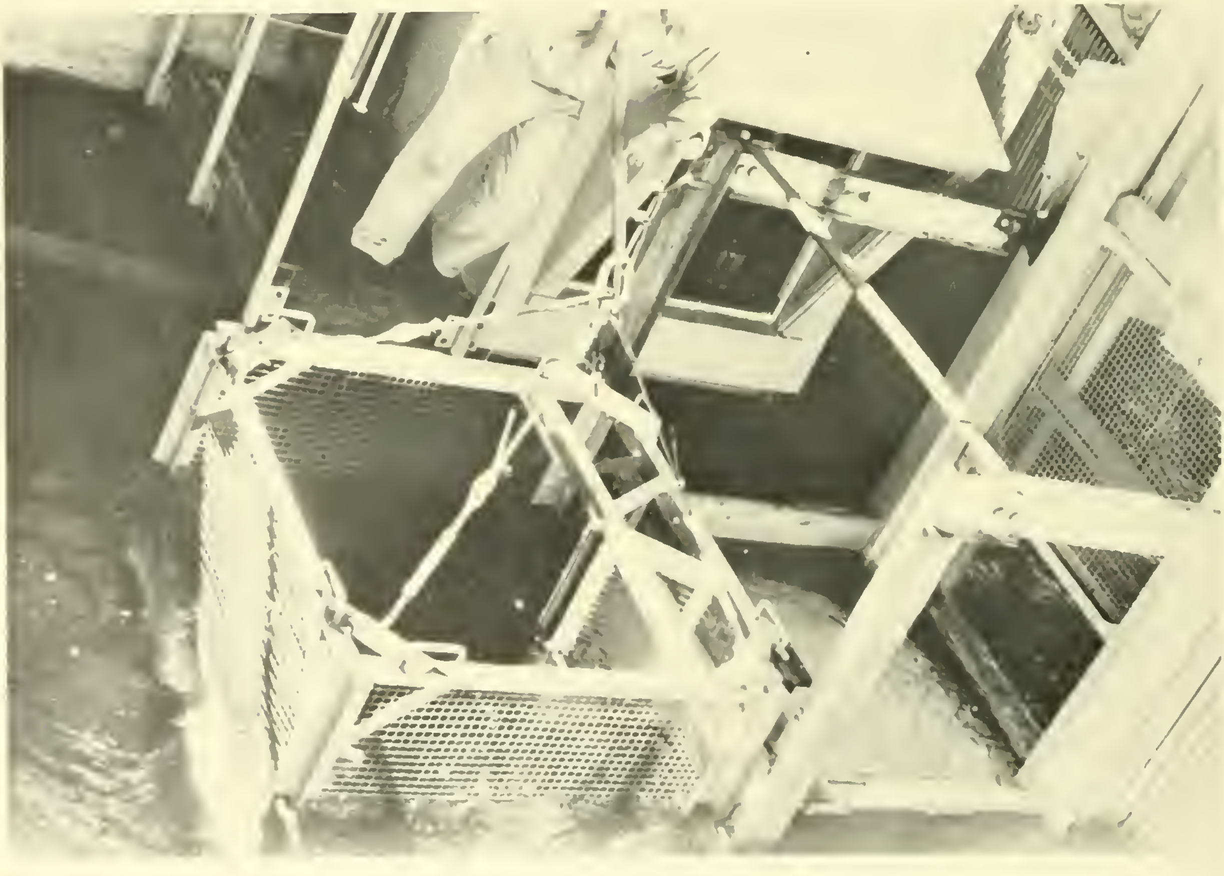

FIGURE 2.—Fishway trap, Rock Island Dam.

amount required to maintain the desired pond level, the surplus water flows either over the top of the dam or is released under lifting gates. Increased flow raises the water depth just below the dam and thereby decreases the velocity of water flowing under the gates. Under these conditions, we saw sockeye salmon swim upstream under the gates, especially when the water depth on the wooden apron just below the dam exceeded 12–18 inches. Consequently, the number of fish passing through the fishways was not always a reliable index of the number passing upstream.

Sockeye salmon have been counted and tags observed (when present) at Rock Island Dam since 1933 and at Rocky Reach Dam since 1961. Complete counts are obtained at Rock Island Dam. During midsummer, when sockeye salmon are migrating, the counting gates near the exits of the three fish ladders are open during daylight but closed at night. At Rocky Reach Dam, on the other hand, the counting gate near the exit of the single fish ladder is open 24 hours daily. Fish are counted 50 minutes per hour from 5 a.m. to 9 p.m. The 50-minute counts are multiplied by 1.2 to estimate the total hourly count. A nighttime correction factor is obtained by counting 24 hours per day once a week. All fish-count data from Rocky Reach Dam used in this report have been corrected by both the hourly and nighttime factors.

STREAM FLOW AND TEMPERATURE

The sockeye salmon migration between Rock Island and Zosel Dams is marked by movement from a larger, cooler river to a smaller, warmer stream. Comparative data on stream flow and temperature are, therefore, potentially important to this study. Data provided by the annual surface-water reports of the U.S. Geological Survey show, however, that the flow of both the Columbia and Okanogan Rivers generally decreases during July and August and has no apparent effect on the migration of sockeye salmon from Rock Island Dam to Zosel Dam.

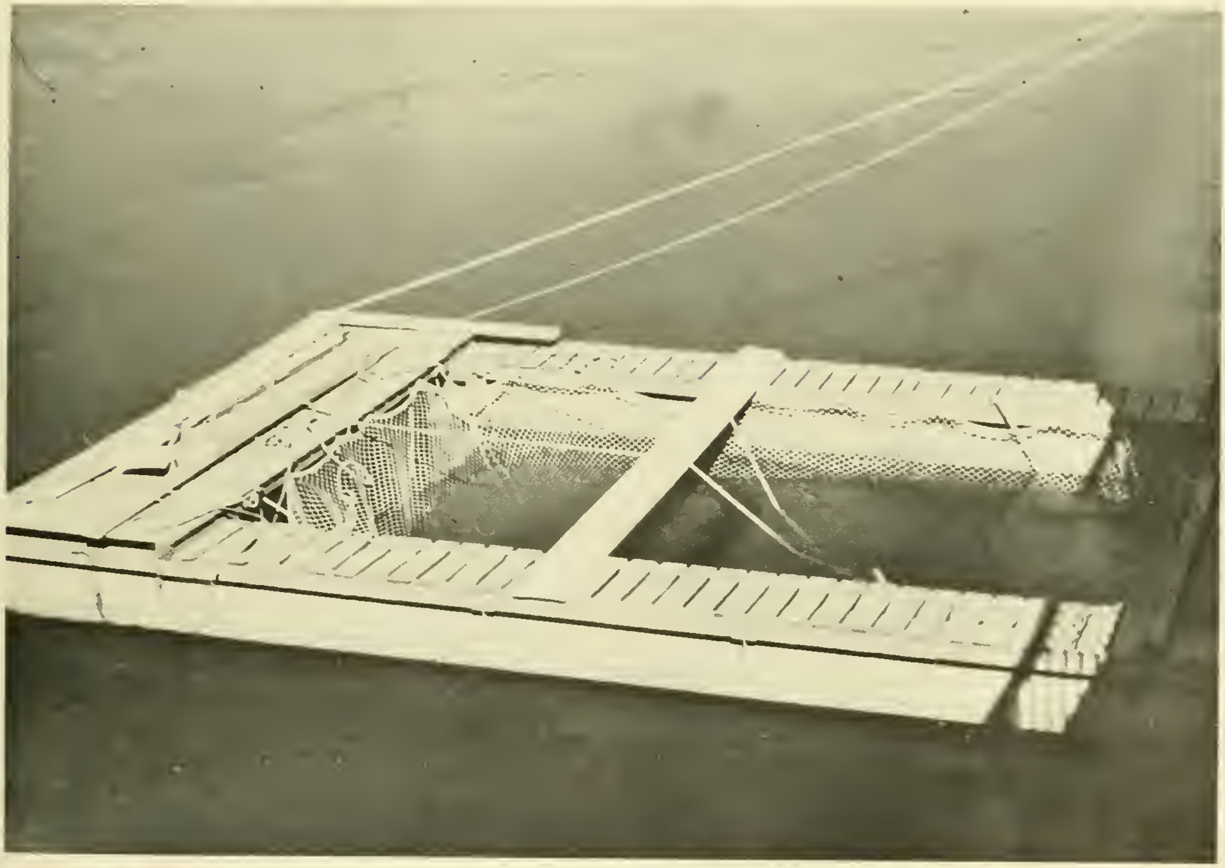

FIGURE 3.—Forebay trap, Rock Island Dam.

Consequently, stream flow is not considered further in our analysis.

It was immediately apparent, on the other hand, from our first observations in 1962 that the water temperature of the Okanogan River greatly influences the migration of sockeye salmon bound for Lake Osoyoos. To understand the effects of temperature better, we have assembled migration-route water temperatures dating back to 1937. Temperature was originally recorded by thermographs or by hand-held thermometers. Daily averages have been computed from the highs and lows on the thermograph charts or from the 8 a.m. and 4 p.m. thermometer readings.

LIMITATIONS AND ADJUSTMENTS OF THE DATA

Before proceeding, it is appropriate to review certain limitations and adjustments of the data that are potential sources of error.

Reliability of the Fish Counts and Tag Observations at Zosel Dam

After 1948, varying proportions of the Okanogan run passed Zosel Dam by means other than the fishways, and the reliability of the counts and tag observations recorded at Zosel Dam since 1948 varies accordingly. We used two criteria to determine which data were adequate for this study. First, by comparing the counts at Zosel Dam with estimates of numbers of fish on the spawning grounds, we calculated the percentage trapping efficiency for 1952–57 and 1962—years for which both fish counts and spawning ground estimates were available. These percentages, however crude, are our best estimates of trapping efficiency at Zosel Dam. Second, we determined from the detailed notes maintained by the fish counters at Zosel Dam whether the modal counts corresponded to the modal numbers estimated to be passing the dam.

Estimates of trapping efficiency are shown in table 2. The overall accuracy of the fish counts in 1955–57 was severely limited. Equally important, the modal counts for those years did not correspond to the modal numbers estimated to be passing the dam. We have accordingly deleted the 1955–57 data from our analysis. Although trapping efficiency was not much higher in 1952, 1954, and 1962, the modal counts agreed closely with the numbers estimated by the counters to be available below the dam. The data for 1952, 1954, and 1962 have been retained, therefore, and, together with the data of high-efficiency years, 1937, 1944, 1953, and 1963, constitute the basis of our evaluation of the effect of water temperature on the migration of sockeye between Rock Island and Zosel Dams. Although no spawning ground estimate was made in 1963, our regular observations indicated a relatively high trapping efficiency at Zosel Dam for that year. A fish-tight weir enabled the counters to make complete fish counts in 1935–37 and 1944. Although the counts of fish were complete in 1935 and 1936, we cannot use them here because there are no water temperature records for those years.

Table 2.—*Information on the efficiency of the trapping system at Zasel Dam*

Year	Count of sockeye at Zosel Dam	Spawning-ground estimate[1]	Trapping efficiency
	Number	*Number*	*Percent*
1952	3,217	25,000	13
1953	67,542	34,260	High
1954	3,760	13,206	28
1955	4,130	47,930	9
1956	668	39,256	2
1957	2,019	25,350	8
1962	944	6,405	15

[1] Tufts, Dennis F., and Donovan R. Craddock. 1963. Spawning escapement of Columbia River sockeye salmon (*O. nerka*), 1962. U.S. Bur. of Comm. Fish. Biol. Lab., Seattle, Wash., 17 pp., Jan 1963 (Processed).

Adjustment of the Tagging Data

French and Wahle (1960) estimated that, before the construction of Rocky Reach Dam, 10.7 days were required for sockeye salmon to migrate from the forebay of Rock Island Dam to Zosel Dam. Their estimate was based on a small sample of 30 tagged sockeye salmon that had been released just above Rock Island Dam in 1954 and 1955 and later observed at Zosel Dam.

To estimate migration time, we have used the large numbers of tagged sockeye salmon (334 and 215) that were released just *below* Rock Island Dam in 1953 and 1954, and later observed at Zosel Dam. Tagged sockeye salmon were released above Rock Island Dam in 1962 and 1963. An adjustment was obviously necessary before the travel time to Zosel Dam of tagged fish that had been released below Rock Island Dam could be compared with the travel time of tagged fish that had been released above Rock Island Dam. We adjusted the data according to the day or days when the number of tagged fish which had been released below Rock Island Dam peaked at the counting stations of Rock Island Dam. The dates of these peaks were treated as dates of release in the forebay. For example, sockeye that had been released below Rock Island Dam on August 2, 1953, peaked at the Rock Island counting stations on August 4, 1953. In our analysis, therefore, we treated this tagged lot as though it had been released in the Rock Island forebay on August 4. This adjustment made it possible to treat all tagged lots in all years as if they had been released in a common location—the forebay of Rock Island Dam.

Water Temperatures Along the Migration Route

Records of temperatures are frequently lacking from the Okanogan River at Monse and the Columbia River at Brewster, near their confluence, but are available instead from Oroville on the Okanogan River and from Rock Island Dam and Bridgeport on the Columbia River (fig. 4). Certain features are clearly evident in figure 4. First, in July and August the Okanogan River is considerably warmer than the Columbia River. Second, in terms of trends (rises and falls over a period of several days) the readings at Oroville and Rock Island (or Bridgeport) reflect the situation in the two streams near their confluence. The absolute readings vary considerably within a river, however, particularly in the Okanogan River, where daily differences occasionally reach 4 or 5° F. (neither station was regularly the higher). Caution must be used, therefore, in comparing the absolute readings from the Oroville and Monse stations.

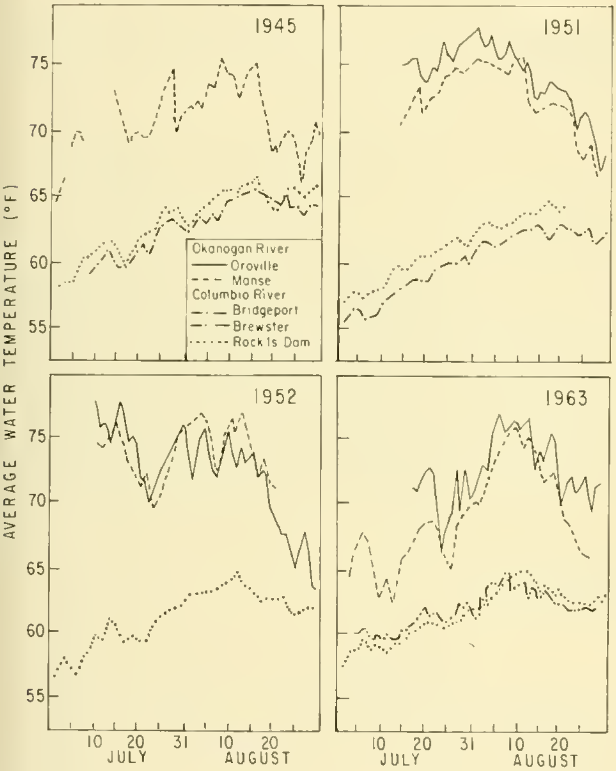

Figure 4.—Comparison of Columbia and Okanogan River temperatures, 1945, 1951, 1952, and 1963.

The methods we describe are not rigorous, and our data are not precise. Yet we believe them to be adequate for the purposes of this report.

TRAVEL TIME BETWEEN DAMS

Travel time of sockeye salmon from Rock Island Dam to Zosel Dam was estimated in 1953 and 1954 before Rocky Reach Dam was built and in 1962 and 1963 after construction. Travel time from Rock Island Dam to Rocky Reach Dam was measured in 1962 and 1963, after Rocky Reach Dam was built.

TRAVEL TIME BETWEEN ROCK ISLAND AND ZOSEL DAMS

In the examination of the basic tagging data for this phase of the study (tables 3–4 and figs. 5–6), attention should be given first to the years before Rocky Reach Dam was constructed. In 1953 the sockeye salmon that had been tagged below Rock Island Dam on July 31, August 1, and August 2, peaked at Rock Island Dam on August 2, 3, and 4 in that order, and at Zosel Dam 6, 9, and 9 days later. The tagged fish that were released below

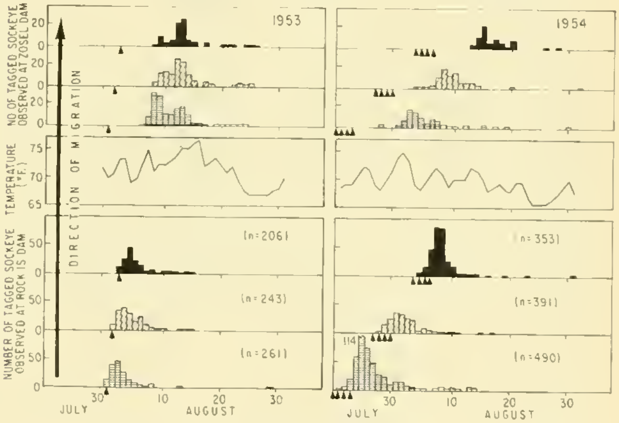

Figure 5.—Number of tagged sockeye observed at Rock Island and Zosel Dams after release below Rock Island Dam in 1953 and 1954. The dates of release are designated by triangles below the base lines and the number of fish released is given in parentheses. Daily average temperature of the Okanogan River is given in the center panel.

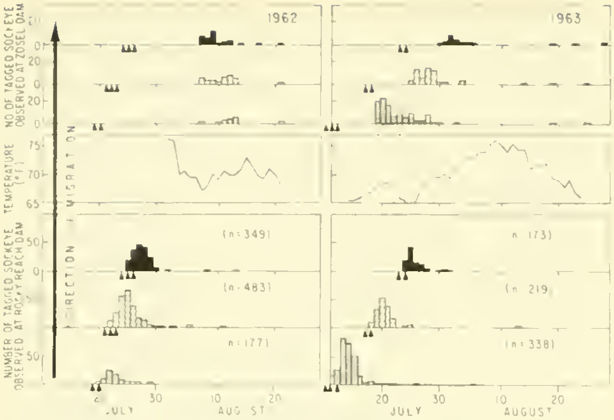

FIGURE 6.—Number of tagged sockeye observed at Rocky Reach and Zosel Dams after release in the Rock Island forebay in 1962 and 1963. The dates of release are designated by triangles below the base lines and the number of fish released is given in parentheses. Daily average temperature of the Okanogan River is given in the center panel.

Rock Island Dam in 1954 have been grouped because of the small numbers which were observed at Zosel Dam. These grouped releases peaked at Rock Island Dam on July 25, July 31, and August 7 and at Zosel Dam 8 to 9, 7 to 8, and 7 to 8 days later.

After Rocky Reach Dam was built, certain changes appeared in the travel time. Tagged sockeye salmon that had been released in the Rock Island forebay on July 19–20, 21–23, and 24–26, 1962, appeared in greatest numbers at Zosel Dam on August 11–13, 7–13, and 7–12. Travel times for the three groups were 22 to 25, 15 to 23, and 12 to 16 days, respectively. The travel times in 1963, on the other hand, were similar to those before Rocky Reach Dam was built—the releases of July 10–12, 17–18, and 23–24 appeared in greatest numbers at Zosel Dam after 7 to 11, 8 to 12, and 8 to 9 days, respectively.

TABLE 3.—*Number of tagged sockeye salmon observed at Rock Island and Zosel Dams after release below Rock Island Dam, 1953 and 1954*

Date of tagging	Number tagged	Point of observations	Date of observation																				
			July											August									
			21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10
1953																							
July 31	261	Rock Island											12	39	45	27	13	9	4	2	5		
		Zosel Dam																	1	8	28	26	11
Aug. 1	243	Rock Island												9	36	40	30	18	24	9	5	4	3
		Zosel Dam																			4	11	12
Aug. 2	206	Rock Island													12	24	46	22	16	3	5	2	4
		Zosel Dam																			1	8	3
1954																							
July 20–23	490	Rock Island	2	6	19	57	114	73	47	26	22	10	11	11	5	3	1	1	..	2	3	1	3
		Zosel Dam								2			2	6	16	14	9	4	7	6	3	1	1
July 27–30	391	Rock Island								2	16	25	35	34	25	23	3	8	5	2	2	1	1
		Zosel Dam														1	1	1	2	9	17	10	13
Aug. 3–6	353	Rock Island															7	19	48	96	84	26	18
		Zosel Dam																					

TABLE 3.—*Number of tagged sockeye salmon observed at Rock Island and Zosel Dams after release below Rock Island Dam, 1953 and 1954—Continued*

Date of tagging	Number Tagged	Point of observation	Date of observation																			
			August																			
			11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1953																					
July 31	261	Rock Island			1																1		
		Zosel Dam	10	16	17	10	3	3	2		1	1	1	1	2	2							
Aug. 1	243	Rock Island			1	1	1																
		Zosel Dam	10	24	21	10	4		4	1				1	3	1	2						
Aug. 2	206	Rock Island	3	2	1	2	1																
		Zosel Dam	5	21	24	5	4	1	3			1	1	1		2	2	1					
1954																							
July 20–23	490	Rock Island	1		4	2		1															
		Zosel Dam		2			3		1		1											1	
July 27–30	391	Rock Island	1				1		1														
		Zosel Dam	5	5	5	2						1											1
Aug. 3–6	353	Rock Island	1	4	4	4		1			1				1								1
		Zosel Dam			3	10	20	5	8	5	2	7						1		2			

The travel times between Rock Island and Zosel Dams are summarized in table 5. In view of the discrepant results of 1962 and the confinement of the 1953 tagging to the end of the run, the effect of Rocky Reach Dam on the travel time between Rock Island and Zosel Dams is best obtained from the records for 1954 and 1963. The travel times tended to be slightly longer in 1963 than in 1954, but the significance of this small difference is questionable.

In any event, the difference between travel times in 1963 and 1954 is greatly overshadowed by the difference between 1962 and 1963, after Rocky Reach Dam was completed. The travel time in 1962 was much the longer and varied erratically within the season—decreasing as the season progressed. This variability was not evident at Rocky Reach Dam, where the appearance of the various tagged lots was orderly in both years (fig. 6). It is appropriate, however, to examine in greater detail

TABLE 5.—*Travel time of tagged sockeye salmon from Rock Island Dam to Zosel Dam, 1953, 1954, 1962, and 1963*

Year	Date of tagging[1]	Best estimate of travel time
		Days
Pre-Rocky Reach:		
1953	Aug. 2	6
	Aug. 3	9
	Aug. 4	9
1954	July 25	8-9
	July 31	7-8
	Aug. 7	7-8
Post-Rocky Reach:		
1962	July 19-20	22-25
	July 21-23	15-23
	July 24-26	12-16
1963	July 10-12	7-11
	July 17-18	8-12
	July 23-24	8-9

[1] For 1953 and 1954, the dates are those when tagged fish which had been released below Rock Island Dam reappeared in peak numbers at the counting stations of Rock Island Dam.

TABLE 4.—*Number of tagged sockeye salmon observed at Rocky Reach and Zosel Dams after release in the Rock Island Dam forebay, 1962 and 1963*

Date of tagging	Number tagged	Point of observation	Date of observation																				
			July																		
			11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1962																							
July 19-20	177	Rocky Reach	---	---	---	---	---	---	---	---	---	4	10	24	16	8	5	5	1	---	1	---	---
		Zosel Dam	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
July 21-23	483	Rocky Reach	---	---	---	---	---	---	---	---	---	---	---	12	26	55	66	39	18	13	2	1	1
		Zosel Dam	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
July 24-26	349	Rocky Reach	---	---	---	---	---	---	---	---	---	---	---	---	---	---	20	38	48	43	22	6	---
		Zosel Dam	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1963																							
July 10-12	338	Rocky Reach	18	24	82	73	50	17	2	6	1	1	1	1	---	---	---	1	---	---	---	---	---
		Zosel Dam	---	---	---	---	---	---	---	---	20	23	16	7	8	6	9	3	3	8	1	1	---
July 17-18	219	Rocky Reach	---	---	---	---	---	---	---	10	34	53	39	7	---	1	2	---	---	---	---	---	---
		Zosel Dam	---	---	---	---	---	---	---	---	---	---	---	---	---	---	3	13	5	15	12	1	1
July 23-24	173	Rocky Reach	---	---	---	---	---	---	---	---	---	---	---	---	---	20	43	13	12	5	---	2	4
		Zosel Dam	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2	3

TABLE 4.—*Number of tagged sockeye salmon observed at Rocky Reach and Zosel Dams after release in the Rock Island Dam forebay, 1962 and 1963—Continued*

Date of tagging	Number tagged	Point of observation	Date of observation																											
			August																									
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1962																														
July 19-20	177	Rocky Reach	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	---	---	---	---	---	---	1	---	---	1	3	4	5	---	---	---	---	---	---	---	2	---	---	---	---	---	---	---
July 21-23	483	Rocky Reach	---	1	---	---	5	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	---	---	---	---	---	---	6	3	3	2	6	7	5	---	---	---	---	---	---	---	1	---	---	---	---	---	---	---
July 24-26	349	Rocky Reach	1	---	---	---	---	---	---	2	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	---	---	---	---	---	---	8	6	3	1	3	4	---	2	---	---	2	---	---	---	1	---	---	---	---	---	---	---
1963																														
July 10-12	338	Rocky Reach	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1	---	---	---	---	---	1	---	---	---
July 17-18	219	Rocky Reach	---	---	---	---	---	---	---	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	---	---	4	---	---	---	---	---	---	---	---	---	---	1	---	---	---	---	1	---	---	---	---	---	1	---	---	---
July 23-24	173	Rocky Reach	2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
		Zosel Dam	9	5	2	2	1	---	---	---	---	---	---	---	---	---	---	---	---	---	1	---	---	---	1	---	---	---	---	2

the movement of tagged fish between Rock Island Dam forebay and Rocky Reach Dam in 1962 and 1963.

TRAVEL TIME BETWEEN ROCK ISLAND AND ROCKY REACH DAMS

Fifteen lots of tagged fish were released in the forebay of Rock Island Dam in the combined tagging seasons of 1962 and 1963. The reappearance of these lots at Rocky Reach Dam 15 miles upstream varied little; 12 peaked on the second day, 1 on the first day, and 2 on the third day after release.

We plotted the observations of tags at Rocky Reach Dam by 4-hour intervals (fig. 7). Only the tags observed during the first 4 days after release have been included because tagged fish became scarce after the fourth day. Fish tagged on July 17 and 19–21, 1962, have not been included because the precise time that these fish passed Rocky Reach Dam was not recorded. The agreement of the data for the 2 years is extremely close. For each release the greatest numbers of tags were observed at 1 p.m. to 5 p.m. on the second day after release. If we consider 10 a.m. as the average release time and 3 p.m. (the midpoint of the 1 p.m. to 5 p.m. period) on the second day out as the average time when tagged fish passed Rocky Reach Dam, the modal travel time was 53 hours. Diurnal consistency is also evident: seven times in eight the numbers of tags observed increased from the first 4-hour period (5 a.m. to 9 a.m.) to the second (9 a.m. to 1 p.m.), peaked during the third period (1 p.m. to 5 p.m.), and decreased during the last (5 p.m. to 9 p.m.).

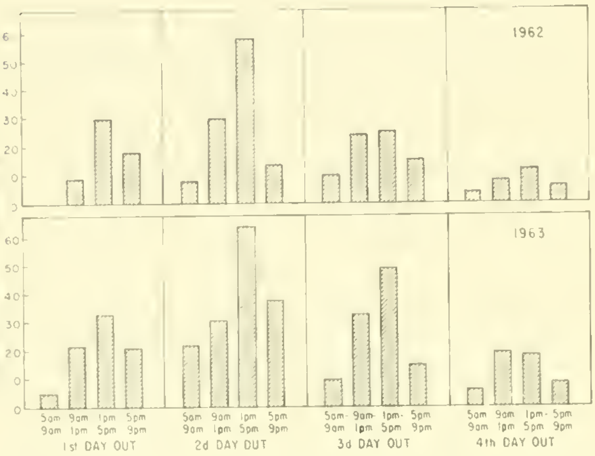

FIGURE 7.—Number of tagged sockeye counted over Rocky Reach Dam in different 4-hour periods during the 4 days after release in the Rock Island forebay in 1962 and 1963. The periods (shown at the bottom of the graph) were 5 a.m.–9 a.m., 9 a.m.–1 p.m., 1 p.m.–5 p.m., and 5 p.m.–9 p.m. Counting was discontinued between 9 p.m. and 5 a.m.

The consistency of the data indicates that fish passage was uniform and orderly at Rocky Reach Dam in 1962 and 1963, and that the much greater travel time from Rock Island Dam to Zosel Dam in 1962 must be attributed to longer travel time above Rocky Reach. Thus, it is necessary to look to the stretch between Rocky Reach Dam and Zosel Dam for the causes of the slow travel time.

EFFECTS OF WATER TEMPERATURE ON THE MIGRATION OF SOCKEYE SALMON

On August 1, 1962, after sockeye had failed to appear at Zosel Dam despite high counts at Rocky Reach Dam, the 133-mile migration route between Rocky Reach and Zosel Dams was searched by plane for schools of salmon. Despite optimum aerial-survey conditions, not a single sockeye salmon was sighted—evidence that the run had not yet entered the Okanogan River.

On August 2, the following day, I (Major) visited the area on the bank of the Columbia River immediately adjacent to the confluence of the Okanogan and Columbia Rivers—a traditional fishing site of the Colville Indians. Of the 8 to 10 Indians present, only 1 responded to questions. He answered that "blueback (sockeye) were milling in the area and fishing was getting better every day."

Sockeye salmon did not reach Zosel Dam until August 7; at that time the counter reported several hundred below the dam and captured 155 in the traps, including 15 with tags. Tag recoveries included individuals from six of the seven lots. This breakdown of the usual chronological order, and the resultant mixing and accumulation of the various segments of the run, indicated that the run had been delayed. Information from the aerial search and from the Indian's report pinpoints the delay at the confluence of the Okanogan and Columbia Rivers.

We hypothesized that the sockeye salmon had been blocked from the Okanogan River by unfavorably high water temperatures until a sharp temperature drop on August 2–3 permitted them to enter the stream on or about August 3 and to reach Zosel Dam on August 7.

To examine the validity of the general hypothesis as it applies to all years, we shall use fish counts and water temperatures along the migration route for 1937, 1944, 1952–54, 1962, and 1963 (table 6 and figs. 8–10). For years when sockeye salmon were tagged (1953, 1954, 1962, and 1963), we will reexamine as part of the analysis the tagging data in figures 5 and 6.

Although the data, particularly the fish counts at Zosel Dam, are not precise enough for us to make a quantitative analysis of the relations involved, we do have evidence pertinent to our hypothesis that unfavorable water temperature (or related factors) blocks the sockeye salmon from the Okanogan River until falling temperatures allow the migration to continue.

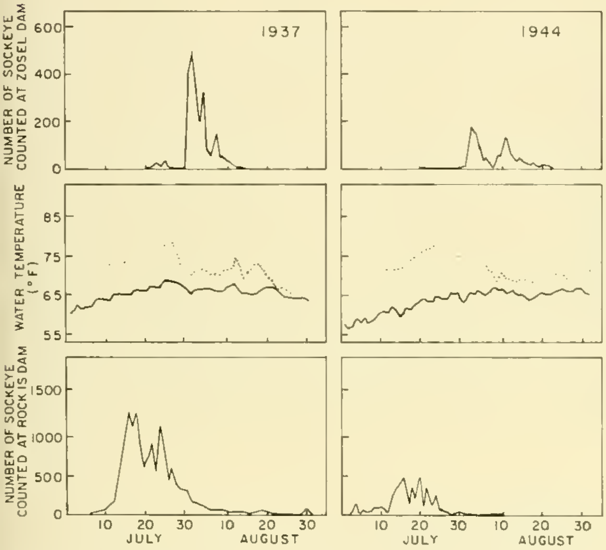

Figure 8.—Number of sockeye salmon counted at Rock Island and Zosel Dams, July and August, 1937 and 1944. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the middle panel.

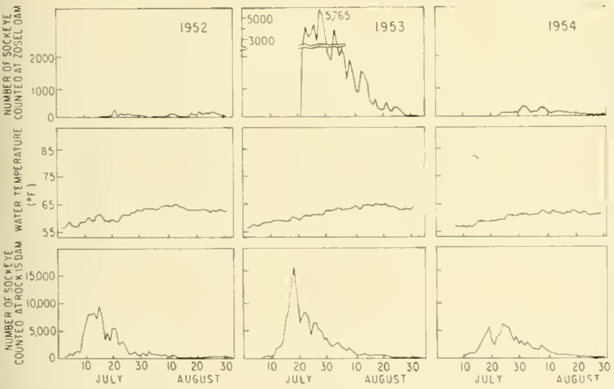

Figure 9.—Number of sockeye salmon counted at Rock Island and Zosel Dams, July and August, 1952, 1953, and 1954. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the middle panel.

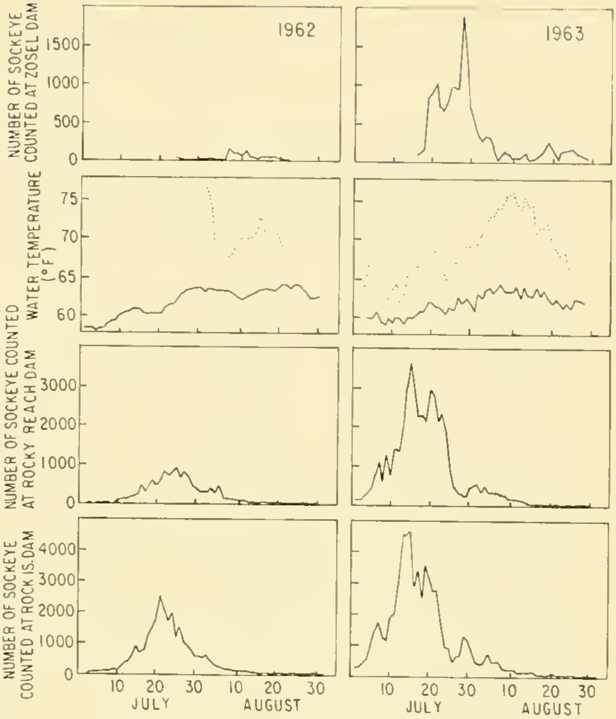

Figure 10.—Numbers of sockeye salmon counted at Rock Island, Rocky Reach, and Zosel Dams in 1962 and 1963. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the second panel from the top.

Figures 8 to 10 establish clearly the general relation between temperature and movement of fish in the Okanogan River. When fish are presumably available to the river, highs and lows in the count at Zosel Dam not evident in the counts at Rock Island Dam or Rocky Reach Dam, regularly follow falling and rising temperature in the Okanogan River. This relation is particularly striking when the temperature drop is preceded by prolonged high temperatures. No influence of the temperature of the Columbia River on the upstream migration of sockeye salmon is apparent.

Knowledge of the normal travel time from Rock Island Dam to Zosel Dam under favorable temperature conditions is highly relevant to an understanding of the effects of unfavorable temperatures

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963*

Date	1937				1944				1952				1953			
	Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.
July 1	0	--------	--------	60.0	3	--------	--------	57.5	68	--------	--------	56.5	--------	--------	66.5	56.0
2	0	--------	--------	60.5	4	--------	--------	56.5	132	--------	--------	56.5	--------	--------	68.0	56.5
3	0	--------	--------	--------	8	--------	--------	57.0	329	--------	--------	57.5	--------	--------	70.0	57.5
4	1	--------	--------	62.5	148	--------	--------	58.5	998	--------	--------	58.5	--------	--------	69.0	57.5
5	1	--------	--------	61.5	56	--------	--------	58.0	739	--------	--------	57.5	--------	--------	70.0	57.0
6	1	--------	--------	62.0	72	--------	--------	59.0	1,019	--------	--------	57.0	5	--------	71.5	57.5
7	1	--------	--------	62.0	60	--------	--------	58.0	1,232	--------	--------	57.0	31	--------	73.5	58.0
8	2	--------	--------	62.5	85	--------	--------	58.5	1,143	--------	--------	58.5	96	--------	73.5	58.5
9	1	--------	--------	64.0	128	--------	--------	59.5	4,777	--------	--------	58.5	146	--------	74.5	58.5
10	0	--------	--------	64.0	126	--------	71.5	60.5	6,810	--------	74.5	59.5	232	--------	74.5	58.5
11	8	--------	72.5	64.0	110	--------	72.0	61.0	8,135	--------	74.0	60.5	375	--------	74.5	59.0
12	13	--------	--------	64.0	58	--------	71.5	60.5	7,981	--------	74.5	59.5	1,626	--------	74.5	59.0
13	156	--------	73.0	64.5	255	--------	70.5	62.0	8,293	--------	75.5	59.5	2,094	--------	73.0	59.5
14	425	--------	73.0	65.5	355	--------	71.5	61.0	7,200	--------	76.0	61.0	2,732	--------	72.5	59.5
15	962	--------	73.0	65.5	402	0	71.5	59.5	9,581	0	76.0	61.5	7,332	--------	73.0	58.5
16	1,317	--------	74.5	65.5	455	--------	72.0	60.5	7,728	0	74.5	60.5	8,201	--------	74.5	58.5
17	1,171	--------	75.0	65.5	170	--------	72.5	62.0	3,797	0	74.0	59.5	11,984	--------	76.0	59.5
18	1,288	--------	74.5	66.0	378	--------	73.5	61.5	4,790	0	73.0	59.5	15,355	--------	76.0	60.5
19	925	--------	73.5	66.5	237	--------	--------	62.5	3,541	0	72.5	59.5	11,348	--------	73.5	60.0
20	670	1	74.0	66.5	460	--------	72.5	63.5	5,435	7	72.5	60.0	6,240	--------	73.5	59.5
21	738	1	73.5	66.5	136	--------	75.5	64.0	5,490	287	71.0	59.5	7,403	10	74.5	59.5
22	929	10	73.5	66.5	398	--------	76.5	63.5	2,644	70	72.5	59.5	8,158	2,090	73.0	60.5
23	595	15	74.0	67.5	137	--------	77.0	63.0	2,850	107	69.5	60.5	7,464	4,175	72.0	61.0
24	1,125	3	76.0	67.5	249	--------	78.0	64.5	2,851	125	69.5	61.5	4,166	3,293	71.0	60.5
25	756	23	77.5	67.5	83	--------	78.0	64.5	2,037	63	70.5	61.5	6,327	3,576	70.0	61.0
26	479	8	77.0	68.5	47	--------	78.0	64.0	847	99	72.0	61.5	6,397	4,463	70.5	61.0
27	622	3	78.0	68.5	66	--------	79.5	64.0	882	90	72.5	62.0	5,191	3,059	71.0	61.5
28	461	3	75.5	68.5	59	--------	80.5	65.0	904	74	73.5	62.0	4,929	5,765	71.0	61.5
29	366	3	74.0	68.0	34	--------	79.0	65.5	490	52	75.5	62.5	3,419	5,180	72.5	61.5
30	268	0	71.0	68.0	38	--------	--------	65.5	403	34	--------	62.5	3,692	3,396	71.5	62.5
31	299	393	--------	67.0	17	--------	74.0	63.0	914	10	--------	62.5	2,953	2,153	70.0	62.5

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963*—*Continued*

Date	1937				1944				1952				1953			
	Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.
Aug. 1	198	494	70.5	66.5	9	0	73.0	63.5	492	11	76.5	63.5	2,161	1,891	70.5	62.5
2	62	343	71.0	65.5	28	4	75.0	65.5	1,321	3	76.0	63.5	2,499	2,823	73.0	62.5
3	80	200	71.5	66.0	12	176	74.0	65.5	907	1	77.0	63.5	2,875	3,959	73.0	63.5
4	100	336	71.5	66.5	14	157	74.5	66.0	874	0	77.0	63.5	2,433	1,984	69.0	63.5
5	101	81	70.5	66.5	11	95	75.5	65.5	726	2	76.0	63.5	1,809	2,310	69.5	63.0
6	79	60	70.0	66.5	6	20	--------	66.5	743	4	74.0	63.5	1,651	2,076	72.5	63.5
7	6	139	70.0	66.5	16	39	71.5	66.5	686	1	73.5	64.0	1,899	1,314	71.5	63.5
8	0	59	70.0	66.0	20	17	71.0	--------	788	0	74.0	64.0	1,462	1,864	71.0	63.5
9	190	35	71.0	66.0	4	2	69.0	66.0	587	13	76.0	64.5	1,177	1,676	72.0	64.0
10	48	14	71.5	66.0	0	54	70.5	65.0	392	68	76.5	64.5	746	950	72.0	64.5
11	47	4	71.5	66.5	1	55	70.0	65.5	250	136	75.5	64.5	444	882	73.0	63.5
12	21	13	74.0	67.5	2	117	--------	65.0	108	55	76.5	65.5	436	1,676	73.5	63.5
13	41	8	72.5	68.0	5	57	70.0	65.0	218	21	77.5	65.0	807	1,551	75.0	64.5
14	53	--------	69.0	66.0	5	19	70.0	64.5	187	2	75.0	64.0	758	1,152	75.0	64.5
15	22	--------	70.5	65.5	3	31	70.0	64.0	183	1	74.5	64.0	487	698	76.0	64.5
16	44	--------	71.5	65.5	7	12	69.5	64.5	116	0	73.0	63.5	361	376	76.5	64.5
17	32	--------	72.5	65.5	4	11	69.5	65.0	101	0	73.5	63.0	333	610	72.0	65.0
18	38	--------	72.5	65.5	3	13	70.0	65.5	138	118	71.5	63.0	287	311	72.5	65.0
19	70	--------	71.5	66.0	1	4	69.0	65.0	114	124	71.5	63.0	226	209	73.5	64.5
20	32	--------	70.5	--------	2	1	69.5	65.0	123	104	71.5	63.0	172	214	72.0	64.5
21	19	--------	--------	67.5	0	5	70.0	65.5	175	201	--------	63.0	74	525	71.0	64.5
22	11	--------	67.5	67.0	2	2	70.5	--------	79	93	--------	63.5	68	292	72.0	64.0
23	18	--------	66.0	66.0	1	0	69.5	--------	42	115	--------	63.0	146	191	69.0	64.0
24	12	--------	66.5	65.5	1	1	70.0	66.0	76	169	--------	62.5	69	335	67.5	64.0
25	8	--------	66.0	64.5	3	1	68.5	66.0	34	148	--------	62.0	47	346	67.0	63.5
26	0	--------	65.3	64.5	0	2	69.0	66.0	46	186	--------	62.5	37	65	67.0	62.5
27	6	--------	65.3	64.0	1	1	69.5	66.5	38	164	--------	62.5	29	28	67.0	62.5
28	3	--------	65.3	64.0	0	--------	70.5	66.5	34	119	--------	62.5	22	74	67.0	63.5
29	0	--------	--------	64.0	1	--------	70.0	66.5	12	13	--------	63.0	60	--------	67.5	63.5
30	79	--------	--------	64.0	0	--------	72.5	--------	14	60	--------	62.5	12	--------	68.0	63.5
31	24	--------	--------	63.0	1	--------	70.5	65.5	9	26	--------	62.5	9	--------	70.0	64.5

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963—Continued*

Date	1954				1962					1963				
	Sockeye		Temperature		Sockeye			Temperature		Sockeye			Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.
July 1	7	--------	64.5	--------	40	0	--------	--------	58.5	285	121	--------	--------	57.5
2	8	--------	64.0	--------	16	0	--------	--------	58.5	287	131	--------	--------	59.0
3	15	--------	66.5	--------	23	4	--------	--------	58.5	484	196	--------	64.0	59.0
4	27	--------	68.5	--------	36	8	--------	--------	58.5	521	299	--------	66.5	59.5
5	39	--------	70.0	--------	54	12	--------	--------	58.0	1,023	406	--------	67.5	59.5
6	93	--------	69.5	--------	69	26	--------	--------	58.5	1,401	732	--------	67.0	50.5
7	136	--------	68.5	56.5	90	28	--------	--------	59.0	1,719	1,123	--------	66.0	59.0
8	182	--------	68.0	57.0	163	22	--------	--------	59.5	1,291	602	--------	64.0	59.5
9	272	--------	69.0	56.5	96	43	--------	--------	60.0	1,238	1,277	--------	62.5	59.0
10	375	--------	65.5	57.0	140	66	--------	--------	60.5	1,819	807	--------	63.5	58.5
11	398	--------	67.0	56.5	292	66	--------	--------	60.5	1,971	1,426	--------	64.0	59.0
12	768	--------	68.0	57.0	389	66	--------	--------	61.5	2,893	1,337	--------	62.0	59.5
13	715	--------	70.0	57.0	416	140	--------	--------	61.0	4,567	2,042	--------	63.0	59.5
14	843	--------	72.0	57.5	638	166	--------	--------	61.0	4,548	2,981	--------	65.5	59.5
15	1,158	--------	73.5	58.5	932	235	--------	--------	61.5	4,601	3,636	--------	65.5	59.5
16	2,383	--------	74.5	58.5	745	415	--------	--------	61.5	2,986	2,891	114	66.0	60.5
17	3,396	--------	74.5	58.5	788	334	--------	--------	61.0	3,300	2,367	148	67.0	60.5
18	4,368	--------	74.0	58.5	1,272	474	--------	--------	60.5	2,653	2,321	187	67.0	60.5
19	5,440	--------	72.5	58.5	1,587	553	--------	--------	60.5	3,572	2,171	810	68.0	61.0
20	3,417	--------	68.0	58.5	1,733	454	--------	--------	61.0	3,116	2,888	898	68.5	61.0
21	2,136	--------	68.5	58.5	2,541	571	--------	--------	61.0	2,734	2,783	1,018	68.5	61.5
22	3,778	--------	69.0	58.5	2,133	800	--------	--------	61.5	2,725	2,127	766	68.0	61.5
23	4,178	9	69.0	59.5	1,702	708	--------	--------	62.5	1,814	2,308	626	66.0	61.5
24	5,908	117	70.5	59.5	1,956	803	51	--------	62.5	886	1,901	776	65.5	60.5
25	5,811	101	72.0	59.5	1,237	856	32	--------	62.5	841	932	971	64.0	60.5
26	5,584	110	71.5	60.5	1,544	683	1	--------	63.0	475	438	968	65.5	60.5
27	4,137	87	69.0	60.5	1,160	793	1	--------	63.5	633	315	934	68.0	60.5
28	3,347	74	68.0	60.5	880	670	8	--------	64.0	1,015	307	1,900	68.5	61.0
29	3,753	61	69.5	60.5	853	480	0	--------	64.0	1,267	215	1,233	69.5	62.0
30	2,815	117	71.0	60.5	573	460	0	--------	63.0	1,138	479	768	69.5	62.0
31	2,913	226	73.5	61.0	666	315	0	--------	62.5	753	546	482	70.0	62.0

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Rams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963—Continued*

Date	1954				1962					1963				
	Sockeye		Temperature		Sockeye			Temperature		Sockeye			Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.
Aug. 1	2,158	386	74.5	61.5	503	344	0	76.5	62.5	490	594	356	69.5	62.0
2	2,573	311	73.0	61.5	583	365	0	76.0	61.5	380	198	281	71.0	62.0
3	1,654	159	69.0	61.5	489	298	0	70.0	62.0	491	484	305	71.5	62.5
4	1,506	88	68.0	61.0	360	232	2	70.5	62.5	706	327	248	73.0	63.0
5	1,542	130	69.5	61.0	273	400	2	69.5	61.5	513	309	83	73.0	63.5
6	1,415	146	71.0	61.5	196	139	16	69.5	62.0	469	339	20	74.0	64.0
7	1,832	234	72.0	61.5	174	142	155	67.5	62.0	360	241	101	74.0	64.0
8	1,575	280	71.0	62.0	168	112	102	68.0	62.5	222	219	149	75.5	64.5
9	1,317	234	68.5	62.5	94	109	100	70.0	61.5	242	183	31	76 0	64.5
10	975	126	70.0	62.0	76	73	61	69.5	61.0	197	172	29	75.0	64.5
11	913	106	70.0	61.5	116	61	135	70.5	60.5	152	128	38	74.0	--------
12	752	103	70.0	61.5	116	73	96	70.0	60.5	132	78	0	75.5	--------
13	527	116	72.0	62.5	100	81	46	70.0	61.5	154	68	43	74.5	64.5
14	718	118	71.5	62.0	67	61	11	71.0	61.5	192	51	116	74.5	63.5
15	502	104	70.0	61.5	65	50	31	73.0	62.0	189	42	42	71.0	63.5
16	332	47	68.0	61.5	101	46	17	71.5	62.0	58	55	47	71.5	64.0
17	320	57	68.5	61.5	59	45	15	70.0	62.5	74	37	12	71.5	63.5
18	349	45	69.0	62.0	65	54	3	69.5	62.0	70	10	159	72.0	63.0
19	279	42	68.0	62.0	52	18	14	71.0	62.0	67	9	257	69.5	63.5
20	177	46	68.0	62.5	63	18	6	70.0	62.5	51	12	107	69.0	62.5
21	129	--------	69.5	62.5	43	17	24	68.5	62.5	71	16	36	68.0	62.5
22	173	--------	69.5	62.0	61	22	15	--------	62.5	48	8	117	69.0	62.5
23	105	--------	66.5	61.5	38	15	--------	--------	62.5	55	4	141	67.0	62.5
24	144	3	65.5	62.0	30	42	--------	--------	62.5	33	4	166	66.0	62.5
25	67	12	65.5	61.5	38	14	--------	--------	62.5	38	29	170	--------	62.5
26	78	26	65.5	60.5	29	8	--------	--------	62.5	53	5	125	--------	62.0
27	54	10	66.0	61.0	54	8	--------	--------	61.5	28	26	108	--------	63.0
28	44	10	67.0	61.0	39	18	--------	--------	61.5	32	52	99	--------	62.5
29	40	9	68.0	61.5	38	9	--------	--------	61.5	28	9	48	--------	62.5
30	39	14	69.5	61.5	36	11	--------	--------	62.0	13	49	--------	--------	63.0
31	33	17	67.5	62.0	17	8	--------	--------	62.5	12	25	--------	--------	63.5

on the migration of sockeye salmon. As has been brought out earlier, the travel time was 8 to 9, 7 to 8, and 7 to 8 days for the three groups tagged in 1954 before Rocky Reach Dam was constructed. In 1963, after Rocky Reach Dam was completed, the most frequent time was 9 days. On the basis of these travel times, we may assume that the sockeye salmon arrive at the mouth of the Okanogan River, 80 miles above Rock Island Dam or roughly halfway on the 154-mile distance from Rock Island Dam to Zosel Dam, on the fourth or fifth day after passing Rock Island Dam. Accordingly, the remaining 3 to 5 days of the typical 8- or 9-day total migration time are spent negotiating the 74-mile route from the confluence to Zosel Dam.

Under this assumption, we can retrace the migration of certain segments of the runs in several years. In 1937, for example, fish were abundant at Rock Island Dam beginning July 13. Had the Okanogan-bound segment of this run moved without delay, we would have expected it at Zosel Dam beginning July 21. Yet, the counts at Zosel Dam remained practically nil until July 31—3 days after the temperature of the Okanogan River began a sharp decline. Prior to July 28, the temperature had been either relatively stable or climbing sharply; either condition apparently delayed the fish some as long as 10 days.

The events of 1937 were essentially repeated in 1944; fish counts increased significantly at Rock Island beginning July 13, 1944, but not at Zosel Dam until August 3—5 days after the water temperature decreased on July 29 and up to 13 days later than expected. Then, following several days of high counts, the number of sockeye salmon arriving at Zosel Dam dropped sharply, finally reaching a low of two fish on August 9. These low counts corresponded with rising or stable water temperatures. The count surged again on August 10—3 days after a sharp drop in water temperature.

Fish migration was similar in 1952. Counting of fish began at Zosel Dam on July 15, but no sockeye salmon were seen until the evening of July 20, when seven were taken in the traps. The count increased markedly the next day, and sockeye salmon were relatively abundant the following 9 days. This increased abundance of fish began 5 days after the beginning of a temperature drop which eventually lasted 9 days. Then, beginning July 25, the temperature rose steadily until August 5, when it began to decline. This second rise in temperature brought a second period of low counts which lasted until August 10—5 days after the temperature fell on August 5. Movement was suppressed a third time by a general 6-day rise in temperature from August 8 to 13. A decrease of temperature on August 14 resulted in a surge of fish at Zosel Dam on August 18—4 days later. Thereafter, the temperature dropped steadily and, judging by the counts, fish migration through the area was unimpeded.

The counts at Zosel Dam in 1953 generally reflected the counts at Rock Island. This agreement probably occurred because increases in water temperature were short (2–4 days) and were followed by falling temperatures during the time when the greater portion of the run was migrating through the critical area.

A late-season temperature rise on August 6–7, 1953, coincided with the arrival of tagged fish. This event provides the first opportunity to study the effects of water temperature in terms of a marked segment of the population. For this analysis, we need to refer to figure 5, which depicts the Okanogan River temperatures and the movement of tagged fish from Rock Island to Zosel Dam. On the assumption that the normal travel time from Rock Island Dam to the confluence of the two rivers is 4 to 5 days, we reason that some individuals from the lot tagged on July 31 reached the confluence on August 4 or 5, before the temperature rise of August 6–7. These early arrivals peaked initially at Zosel Dam on August 8. The rising water temperatures on August 6–7 suppressed entry of the later arrivals into the Okanogan River until a drop of temperature on August 8. This decrease of temperature resulted in another surge of tagged fish at Zosel Dam on August 11 to 12, and gave the count of tagged fish at Zosel a bimodal distribution not evident at Rock Island. Apparently, few fish from the lot tagged on August 1 arrived at the river mouth before the temperature rose; most arrived during the rise of August 6 to 7 and therefore did not appear at Zosel Dam until August 12—4 days after the temperature fell on August 8. Similarly, few fish from the lot tagged on August 2 arrived at the confluence before the temperature rise suppressed their entry. Most of these fish arrived at Zosel Dam on August 12 to 13—4 or 5 days after the temperature drop.

The movement of the various tagged segments of the 1954 run can also be retraced from figure 5.

Fish released below Rock Island Dam on July 20–23 peaked at Rock Island Dam on July 25, and at Zosel Dam on August 2–3, 8 to 9 days later. From these records we infer that most of the tagged fish reached the Okanogan River on July 29, when the temperature was just beginning to increase, and that this increase did *not* suppress entry to the stream. Similarly, the collective releases of July 27–30 peaked at Rock Island Dam on July 31 to August 1 and at Zosel Dam on August 8. On the assumption of 4 days for travel, we estimate that most of these fish arrived at the mouth of the Okanogan on August 5–6 when the temperature began a new rise. Again, however, migration was not affected. Finally, the August 3–6 releases of tagged fish peaked at Rock Island Dam on August 7–8 and probably arrived at the mouth of the Okanogan River on August 11–12, when temperatures were fairly stable. These fish also appear to have migrated freely through the Okanogan River. A possible explanation of the normal progress of the migration despite rising temperatures is given below in our discussion of the 1963 migrations.

Temperatures of the Okanogan River were not recorded in 1962 until August 1. High air temperatures indicate, however, that the water temperature almost surely had been rising prior to August 1. Rising temperature would account for the July 26 to August 5 lull in the count at Zosel Dam (figs. 6 and 10). On the basis of counts at Rocky Reach Dam, we would have expected the arrival of sockeye salmon, both tagged and untagged, at Zosel Dam during this interval. The arrival of the fish at the mouth of the Okanogan River coincided, however, with rising water temperatures, a condition which apparently blocked their entry.

The 1963 migration progressed from Rocky Reach Dam to Zosel Dam without major delay (figs. 6 and 10). Tag recoveries were orderly in contrast to those of 1962; peaks at Zosel Dam followed comparable peaks at Rocky Reach Dam by 6, 6 to 8, 6, 7 to 9, 6 to 9, and 6 to 10 days. Thus, migration was normal in 1963, despite generally rising water temperatures.

The absence of delay in 1954 and 1963, despite rising water temperatures, focuses attention on the importance of the level at which the temperature is changing. For example, migration was unimpeded by rising temperatures in the 62° to 69° F. range in 1963, but was halted by rises in the 75° to 78°, 70° to 77°, and 74° to 78° F. ranges in 1952.[2] Furthermore, a temperature rise in the 73° to 78° F. range at Oroville interrupted the migration in 1937, a year in which occasional temperature readings taken at Monse on the lower Okanogan River were even higher than those at Oroville (Chapman, 1941). On the other hand, the 1954 migration was apparently unaffected by rises in the 68° to 70° F. range. The dependability of the latter example is subject to some question, however, because the temperature readings were recorded at Oroville, not at Monse.

These several examples suggest a threshold temperature of about 70° F., below which migration is not affected, but above which rising or stable temperatures inhibit migration—a condition which endures until a sharp drop allows the migration to resume.

We have not considered here a situation in which fish enter the Okanogan River under favorable conditions only to be confronted enroute by sharply rising water temperatures. We have no data on this aspect of the problem, but suspect that the behavior and survival of the fish depend on several factors, including: (1) their location at the time they are confronted by rising temperatures; (2) their ability to acclimate; (3) their size, general health, and stage of maturity; and (4) the level to which the water temperature rises.

RESULTS OF OTHER STUDIES AND THEIR POSSIBLE BEARING ON THE PROBLEM IN THE OKANOGAN RIVER

The environmental factors that control the migrations of adult Pacific salmon have long been of practical and theoretical interest to fishery biologists. The literature gives many examples of environmental influences that affect different populations in different ways. Rather than present another review of the extensive literature on this broad subject, a matter so capably handled by Hoar (1953) and Allen (1956), we refer here only to the more important papers that deal with the environmental factors that influence the sudden mass movement of migrating salmon.

Several investigators have found that rainfall and streamflow affect the migration of adult salmon. Pritchard (1936), and Davidson, Vaughan, Hutchinson, and Pritchard (1943), who studied pink salmon (*O. gorbuscha*), and Hunter (1959), who worked with pink salmon and chum salmon (*O. keta*), concluded that entry into a river follows increases in stream flow. Shapavalov and Taft (1954) noted a correlation between the general periods of the spawning runs of silver salmon (*O. kisutch*) and rainfall. They further believed, but were unable to demonstrate quantitatively, that fish movement increased with a rise of stream flow. Allen (1956), on the other hand, related the movement of silver salmon and chinook salmon (*O. tshawytscha*) to nighttime rainfall and low barometric pressure, respectively. Ellis (1963) believed that the entry of silver salmon and sockeye salmon into rivers was associated with the appearance of atmospheric warm fronts over the estuary.

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[2] These temperatures, recorded at Monse, are not subject to the possible error of estimating temperatures in the lower river from actual readings at Oroville.

Only Foerster (1929) and Cramer and Hammack (1952) attributed the sudden movement of salmon to changes in water temperature. Foerster, who reported on sockeye salmon at Cultus Lake, British Columbia, noted that the numbers of fish arriving at a counting fence synchronized closely with temperature change; increases in the daily run accompanied declines in temperature. Cramer and Hammack, who studied chinook salmon in Deer Creek, a tributary to the Sacramento River, Calif., concluded that at the close of a period of clear weather and relatively cool water, sudden increases in water temperature to 75° F. caused an upsurge of fish.

Andrew and Geen (1960), in their appraisal of all available information on the possible effects of dam construction on the Fraser River, British Columbia, devoted considerable attention to the effects of temperature and delay on upstream-migrating salmon. High water temperatures, they concluded, are detrimental to salmon in their upstream migration because they increase the rate of energy consumption and the incidence of disease and parasites, and may be directly lethal.

In the matter of delay, Andrew and Geen (1960) cited Thompson (1945) as having shown that a delay of 12 days at Hell's Gate (before construction of the fishways) was sufficient to prevent sockeye salmon from reaching their spawning grounds, and that lesser delays reduced the reproductive capacity of the fish. The same authors also referred to an incident in the Fraser Canyon at Yale, British Columbia, in 1955 where the early run to the Stuart River was blocked 6 days by high water. Of an estimated 30,000 to 35,000 sockeye salmon, only 2,170 reached the spawning grounds.

The effect of delay on the productivity of salmon has been illustrated by studies of fish passage at a rock slide on the Babine River, British Columbia (Godfrey, Hourston, Stokes, and Withler, 1954). Concerning this study, Andrew and Geen (1960) stated:

> . . . Tagging of fish below the point of difficult passage and recovery of the tagged fish at a counting fence 40 miles upstream showed that some of the fish delayed below the obstruction were able to migrate to their spawning grounds but relatively few were able to spawn successfully. Because fish were delayed and weakened below the obstruction they were not able to migrate at a normal rate after passing the obstruction. The effective spawning in 1952, when some sockeye were delayed for extended periods, was estimated as 30 to 42 percent of the numbers of female sockeye that reached the spawning grounds or 7 to 10 percent of the total escapement. From 30 to 40 percent of the female sockeye examined on the spawning ground died unspawned and others died after passing the obstruction but before reaching the spawning grounds.

The previous references indicate that salmon that have been delayed enroute to spawning grounds can be affected in two ways. First, some die enroute to the spawning grounds and second, some complete the journey but are unable to spawn successfully. We conclude that temperature blocks of the type outlined in this paper similarly affect sockeye salmon bound for the Okanogan River spawning grounds.

SUMMARY

Sockeye salmon were tagged at Rock Island Dam and later observed at Zosel Dam on the Okanogan River in 1953–54 and 1962–63. These experiments were used to detect any changes in the migration time caused by Rocky Reach Dam, which was constructed on the migration route during the intervening years.

Travel time varied greatly, both between and within years. The difference between 1962 and 1963 exceeded the difference between 1963 and 1953–54. The best estimate of the time required for sockeye salmon to migrate from Rock Island Dam to Zosel Dam is 7 to 9 days, barring major delay due to environment. This travel time has not been increased by Rocky Reach Dam.

Water temperature of the lower Okanogan River, or factors linked with it, is by far the greatest source of delay. Below 70° F., entry into the Okanogan River is relatively unimpeded. Above 70° F., relatively stable or rising temperatures delay entry until a sharp drop occurs.

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SEASONAL OCCURRENCE AND SIZE DISTRIBUTION OF POSTLARVAL BROWN AND WHITE SHRIMP NEAR GALVESTON, TEXAS, WITH NOTES ON SPECIES IDENTIFICATION[1]

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ABSTRACT

Postlarvae of the genus *Penaeus* were collected at the entrance to Galveston Bay, Tex., over a 4-year period and along Galveston Island's beach during a 1-year period. Postlarval brown shrimp, *P. aztecus*, and white shrimp, *P. setiferus*, were the predominant penaeids caught. Morphological characters, seasonal size differences, and occurrence of juveniles in adjacent nursery areas were used to identify these species. Seasonal occurrence, size distribution, and measures of relative abundance are given for postlarvae of the two species. The uniformity in size of postlarvae from collections along the beach and at the bay entrance indicated that small shrimp do not grow much when they are along the beach.

Shrimp are the most valuable marine fishery resource of the Gulf of Mexico, where commercial landings annually exceed 170 million pounds and are valued at nearly $60 million. Many aspects of the biology and early life history of these crustaceans have been examined; however, the factors causing fluctuations in their abundance must be better defined before optimum management of the shrimp fishery can be realized.

The early life histories of commercially important species of the genus *Penaeus* inhabiting the northwestern Gulf of Mexico are similar. Each spawns in offshore waters, where the planktonic larvae hatch after several hours. During ensuing weeks, the larvae pass through a series of metamorphoses and reach near-shore areas as postlarvae. The young shrimp grow rapidly after moving into estuarine nursery areas, and return to offshore waters to complete their life cycle.

As Bearden (1961) has pointed out, the postlarvae that reach inshore waters represent the success of the spawning season and, after several months of growth, will make up the bulk of the commercial shrimp catch for a given year. Baxter (1963) has shown that systematic sampling of postlarvae entering the major nursery areas can provide an index that is useful for predicting the subsequent abundance of juvenile and adult shrimp on inshore and offshore fishing grounds.

The objectives of this report are to describe trends in the seasonal abundance and size composition of commercial shrimp postlarvae near Galveston Island, and to evaluate the use of seasonal differences in their body lengths as an aid in identifying the various species. Also examined is the question: Do young shrimp use the surf zone as a nursery area? The results of this 4-year study form a basis for current research on the biology and dynamics of the postlarval phase of commercial shrimp populations in the Gulf of Mexico.

SAMPLING PROCEDURE

Studies of postlarval shrimp began as part of a developing investigation of the life history of penaeid shrimp outlined in detail by Kutkuhn (1963). Knowing that shrimp reach shore as postlarvae and

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enter nursery areas through tidal passes, we established a sampling station at the entrance to Galveston Bay in November 1959. Additional stations along Galveston Island's Gulf beach were added later.

GALVESTON ENTRANCE

The initial sampling site was on the south side of the entrance to Galveston Bay (station A, fig. 1), where we collected postlarval shrimp twice each week. This location was not suitable as a sampling station after Hurricane Carla in September 1961. Thereafter, semiweekly samples were obtained from station B, near the base of the north jetty. Bottom materials at both stations consisted of well-compacted sand.

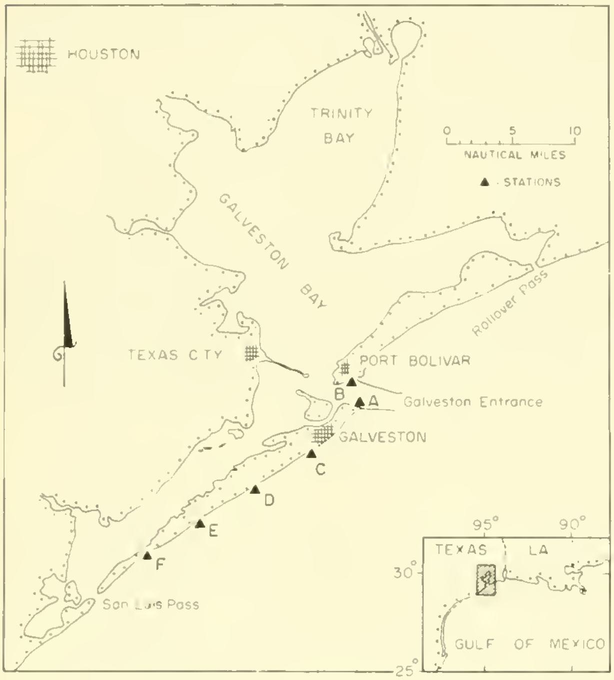

FIGURE 1.—Galveston Island and environs, showing sampling stations.

Collections of postlarvae were made with a 5-foot, hand-drawn beam trawl fitted with a plankton net at its cod end (Renfro, 1963). The wings of the trawl consisted of nylon netting having 50 holes per square centimeter. We believe that escapement of postlarval shrimp was negligible, because most collections contained an abundance of organisms more minute than the smallest postlarvae captured. To test whether or not large shrimp were evading the small beam trawl we towed a fine-mesh, 20-foot seine on several occasions. A standard procedure was followed during each collection. One end of a 150-foot line was tied to a stake driven into the sand at the water's edge. The collector held the free end of this line in one hand and the bridle of the trawl in the other and pulled the gear along the bottom in a semicircular path from the shoreline.

GULF BEACH

Collections of postlarval shrimp were made twice each month between April 1960 and April 1961 at 5-mile intervals along Galveston Island's 25-mile beach (stations C, D, E, and F, fig. 1). The same beam trawl was used at beach stations, but because of the surf, the sampling procedure was altered from that used at stations A and B. The collector waded a measured 75 yards directly offshore, set the gear, and towed it back to shore. Computations of bottom areas sampled were based on distance towed and the dimensions of the net.

At all stations we made meteorological and hydrographic observations. Those that we consider to be pertinent, namely water temperature, salinity, and tidal stage, are listed in appendix tables 1 and 2 along with the numbers of postlarval brown and white shrimp collected on each sampling date.

SEASONAL OCCURRENCE

GALVESTON ENTRANCE

Postlarval brown shrimp, *P. aztecus* Ives, appeared at Galveston Entrance and migrated to the nursery areas within Galveston Bay at about the same time

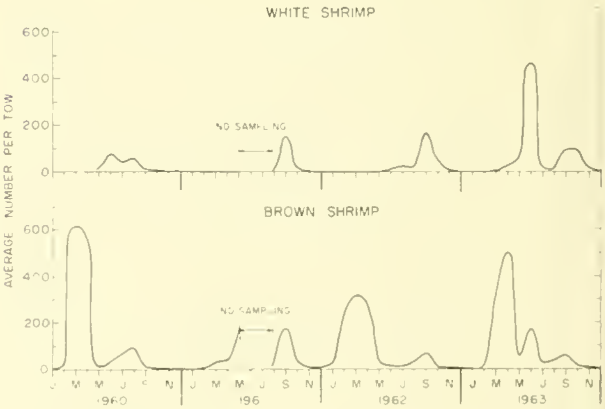

FIGURE 2.—Seasonal abundance of postlarval brown and white shrimp at Galveston Entrance, 1960–63.

during each year of the study (fig. 2). The greatest numbers occurred in the spring; usually peak abundance was reached between mid-March and mid-April. Following the spring peak, comparatively few postlarvae were caught until about mid-June. Thereafter, the number of postlarvae in the collections increased through July and reached a second peak in August or September. In each year, the numbers of brown shrimp postlarvae present at Galveston Entrance diminished rapidly after the second peak and remained low throughout the winter. During 1961, peak abundance appeared to develop in late April and early May, but because sampling was suspended from May 8 to August 11, the actual time of the peak for that year is unknown.

The first postlarval white shrimp, *P. setiferus* (Linnaeus), were taken in early May of each year at Galveston Entrance (fig. 2). Seasonal distribution of postlarval white shrimp suggests that two peaks in abundance may occur each summer and that the relative strength of these peaks is variable.

GALVESTON ISLAND BEACH

Trends in seasonal occurrence of postlarval brown and white shrimp at Galveston Island beach stations were similar to those at Galveston Entrance stations (table 1). Brown shrimp postlarvae were numerous in mid-April 1960, from late June through August, and again during April 1961. In contrast to Galveston Entrance, a few brown shrimp postlarvae were present along the beach during late December and January. In 1961 brown postlarvae did not appear in significant numbers until early March. Postlarval white shrimp were caught in beach samples from mid-May through November 1960 and were most abundant from late June through July. None was taken from December 1960 through April 1961.

Samples of postlarvae were collected along Galveston Island beach to determine if young shrimp use the littoral zone along beaches as nursery areas. Should they use this zone, advanced stages of postlarval shrimp could be expected in collections from beach stations. Agreement as to general size of postlarvae from the beach and from Galveston Entrance (table 2), indicates, however, that postlarvae spend little time in the beach area. Repeated tows with a fine-mesh seine at beach stations caught no shrimp larger than those taken in the beam trawl.

TABLE 1.—*Average monthly densities of postlarval shrimp at Galveston Entrance and Galveston Island beach stations, April 1960–61*

[Figures represent the average number of postlarvae per 100 m.² of bottom in 7 to 12 collections each month]

Month	Brown shrimp postlarvae		White shrimp postlarvae	
	Galveston Entrance	Gulf beach	Galveston Entrance	Gulf beach
1960:				
Apr.	294	52	0	0
May	2	15	6	9
June	23	54	40	52
July	35	234	14	133
Aug.	51	153	29	26
Sept.	0	3	2	39
Oct.	0	3	0	3
Nov.	0	3	0	3
Dec.	1	8	0	0
1961:				
Jan.	0	1	0	0
Feb.	1	1	0	0
Mar.	13	70	0	0
Apr.	72	760	1	0

TABLE 2.—*Mean total lengths of postlarval shrimp collected concurrently along the Galveston Island beach and in Galveston Entrance, 1960–61*

[Figures in parentheses indicate number of specimens measured]

Month	Brown shrimp postlarvae		White shrimp postlarvae	
	Beach	Entrance	Beach	Entrance
	Mm.	*Mm.*	*Mm.*	*Mm.*
1960:				
Apr.	11.4 (82)	11.5 (167)	------	------
May	10.4 (52)	10.5 (34)	6.3 (47)	6.4 (51)
June	8.9 (113)	8.8 (101)	5.9 (115)	6.5 (149)
July	8.7 (181)	8.4 (155)	7.2 (186)	6.3 (129)
Aug.	8.6 (241)	8.5 (146)	6.7 (177)	6.3 (153)
Sept.	9.5 (25)	10.0 (10)	7.5 (77)	7.1 (35)
Oct.	10.1 (27)	11.0 (4)	6.8 (24)	7.2 (10)
Nov.	10.9 (23)	11.2 (6)	7.5 (23)	7.5 (8)
Dec.	11.9 (59)	------	------	------
1961:				
Jan.	11.7 (6)	------	------	------
Feb.	11.0 (11)	12.0 (6)	------	------
Mar.	11.6 (165)	11.6 (86)	------	------
Apr.	11.3 (200)	11.6 (112)	------	------

IDENTIFICATION AND SEASONAL SIZE DISTRIBUTION

Of the three commercially important species of the genus *Penaeus* in the northern Gulf of Mexico, the pink shrimp, *P. duorarum*, is the least abundant. Small numbers of adult pink shrimp are commonly caught off Galveston Island (15–20 fathoms), but landing data compiled by the Bureau of Commercial Fisheries Branch of Statistics[3] included no pink shrimp in landings of 3.7 million pounds taken from Galveston Bay during 1960–63. A few pink shrimp, however, may have been landed and reported as brown shrimp. Of about 47,000 juvenile shrimp examined from Galveston Bay bait landings between January 1960 and December 1963, only 17 (less than 0.04 percent) were pink shrimp. In earlier work, the second author (1958–59) found no pink shrimp among more than 10,000 juvenile penaeid shrimp taken from upper Galveston Bay. Although postlarval pink shrimp obviously occur in the Galveston area they evidently are scarce; all postlarvae we caught were classified as brown or white shrimp.

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[3] "Gulf Coast Shrimp Catch by Area, Depth, Variety, and Size," Annual Summaries, 1960–63.

MORPHOLOGY

No single criterion is sufficient to distinguish brown and white shrimp postlarvae, but they can be separated by taking into account various morphometric characters, relative size, and seasonal occurrence as juveniles in the estuary. Morphological and morphometric differences between postlarval brown and white shrimp provided by Pearson (1939) and Williams (1959) are sufficient to separate these species during most seasons. Williams, working with shrimp from North Carolina, developed a provisional key to early postlarvae. He stated that the tip of the rostrum and the extended third pereiopod on postlarval white shrimp do not extend to the distal edge of the eye. Conversely, in the brown shrimp, both the tip of the rostrum and extended third pereiopod reach to or beyond the edge of the eye. In postlarvae from the Galveston area, these characteristics suffice only to separate postlarval white and brown shrimp with a total length of 10 mm. or less, whereas Williams was able to use them in North Carolina for separating postlarvae up to 12 mm. total length.

OCCURRENCE ON GALVESTON BAY NURSERY GROUNDS

According to our records, brown shrimp are the only postlarval *Penaeus* that enter Galveston Bay during the first 4 months of the year. This observation agrees with findings from several previous studies conducted in the bay. Renfro (1959) found only brown shrimp postlarvae and juveniles (17 mm. and above) in upper Galveston Bay during April and May 1959. Gunter (1960) also found brown shrimp to be the only species at the juvenile stage present in Galveston Bay during April and May 1960. Later reports by biologists of the Texas Game and Fish Commission corroborate the observations of Renfro and Gunter (Pullen, 1962).

By June, advanced postlarval and early juvenile white shrimp (18–28 mm.) become abundant in Galveston Bay, and both brown and white shrimp are present throughout the summer (Gunter, 1960). Additional evidence regarding the identity of the winter and early spring postlarvae was provided in 1960 when 1,200 postlarvae, taken on April 12 at Galveston Entrance, were brought into the laboratory to be reared. All that grew to identifiable size (150) were brown shrimp.

SEASONAL SIZE DISTRIBUTION

The size of postlarvae caught at the entrance to Galveston Bay provides a strong clue to species identity during some seasons (fig. 3). During the winter, the total length of brown shrimp postlarvae ranged from 10 to 14 mm. and averaged 12 mm. (fig. 3). Beginning in May of each year, a second group of much smaller (6.0 to 8.0 mm.) postlarvae appeared in the samples. These shrimp possessed the external morphological characteristics of postlarval white shrimp described by Pearson (1939) and Williams (1959). By late June the length distributions of the two groups of postlarvae began to overlap. The modes of the length distribution of brown postlarvae decreased, possibly because adult brown shrimp were spawning near shore in spring and summer, or because warm water temperatures increased the developmental rates of larvae. During the same period, some white shrimp postlarvae as long as 10.5 mm. entered the estuary. Most of the larger postlarvae, however, exhibited the characteristics ascribed to brown shrimp by Williams (1959). The overlap in length distributions persisted throughout the summer, but the mean length of brown shrimp postlarvae always exceeded that of white shrimp in the same samples (fig. 3). In the latter part of each year, the modal length of brown shrimp postlarvae increased, and by October in some years the overlap in length distributions had ended.

Postlarvae of brown and white shrimp caught at beach stations and at Galveston Entrance were of similar sizes (table 2). The total length of postlarval brown shrimp ranged from 8.5 to 12.0 mm. (mean, 11.5 mm.). White shrimp ranged from 5.0 to 9.5 mm. (mean, 7.0 mm.). No significant difference existed among the mean lengths of postlarvae taken at the various beach stations on the same day.

SUMMARY

Collections of penaeid postlarvae were obtained semiweekly at Galveston Entrance over a 4-year

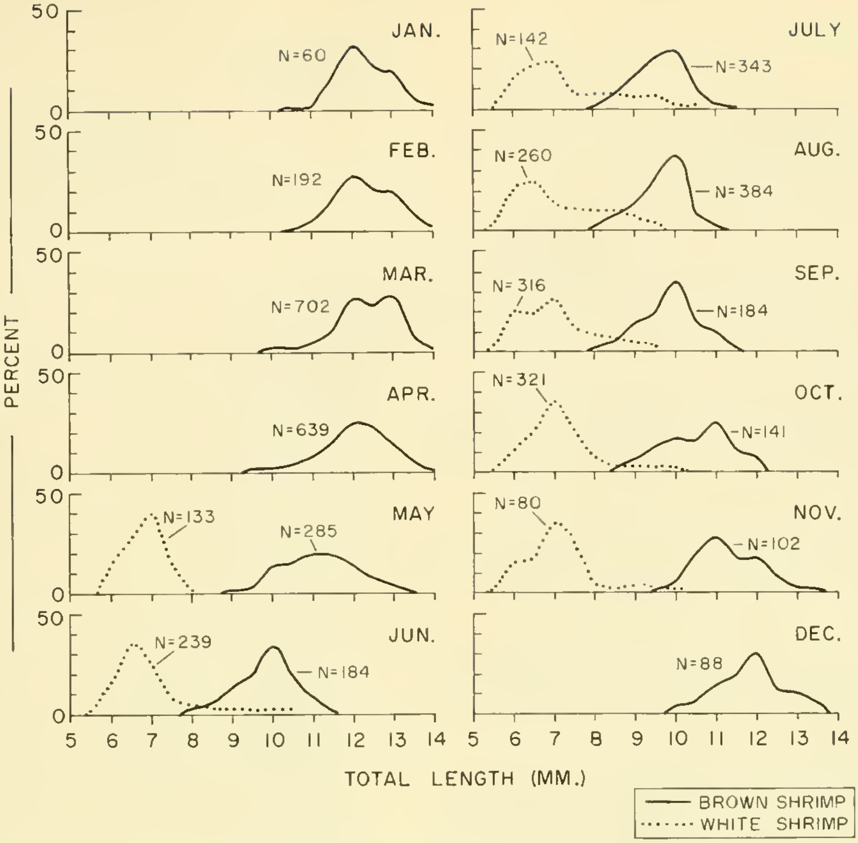

FIGURE 3.—Seasonal size distribution of postlarval brown and white shrimp at Galveston Entrance, 1960–63. (N indicates sample size.)

period and twice each month at four stations along Galveston Island's Gulf beach for 1 year.

Postlarval brown shrimp were collected at Galveston Entrance from February until mid-December of each year. At Galveston beach stations, they were found throughout the year but in smaller numbers during the winter. Numbers of brown shrimp postlarvae reached an annual peak between mid-March and mid-April.

Postlarval white shrimp were first caught at Galveston Entrance and along the beach in May and were most abundant through the summer.

Postlarvae of brown and white shrimp were separated by morphometric characters and by the seasonal occurrence of each species in the adjacent estuary. The brown shrimp was the only *Penaeus* species at the postlarval stage present along the Galveston Island beach and at the entrance of Galveston Bay from December through April. All individuals were relatively large (11 mm. or longer) during this period. After April, their average size decreased, remained relatively small throughout the summer, and then increased again in the fall. White shrimp postlarvae first appeared in May at lengths much shorter than those of brown postlarvae in the same collections; the total lengths of the majority ranged from 6.0 to 8.0 mm. During the summer, the length distributions of postlarvae of brown and white shrimp overlap in the 8- to 10-mm. length range. The two species at this stage of development may, however, be separated by the morphological characteristics described by Pearson (1939) and Williams (1959). At times, the largest white shrimp postlarvae in a sample were longer than the smallest postlarvae of brown shrimp, but the mean lengths of the white postlarvae were always less than those of the brown postlarvae.

The similarity of mean lengths of postlarvae collected along the beach and at Galveston Entrance suggests that significant growth does not occur along the beaches and that the surf zone is not an important nursery area for small shrimp.

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APPENDIX

Table A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°*C.*	o/oo	
1959:						
Nov. 9	1000	0	0	------	------	------
16	1330	0	0	------	------	------
Dec. 11	1500	0	0	------	------	------
18	------	0	0	------	------	------
21	------	0	0	------	------	------
31	------	0	0	------	------	------
1960:						
Jan. 8	------	1	0	------	------	------
13	1530	4	0	15.5	25.3	HWS
15	1100	0	0	14.9	25.3	F
19	1400	0	0	9.8	9.4	E
22	0900	12	0	9.0	23.9	F
25	1100	1	0	10.2	26.0	F
28	1115	1	0	12.5	18.3	F
Feb. 1	1300	1	0	12.2	28.4	------
5	1100	0	0	10.2	14.0	F
9	0900	2	0	15.0	31.2	------
11	0930	0	0	13.0	27.3	E
16	1100	3	0	------	16.9	------
18	1415	3	0	12.5	12.1	E
24	1000	2	0	10.0	23.6	F
25	1500	2	0	12.0	------	F
Mar. 1	1345	0	0	10.0	28.6	F
3	1405	0	0	10.5	11.1	E
7	1620	6	0	10.0	26.2	F
11	1330	53	0	13.0	15.9	E
15	1400	39	0	15.0	25.4	------
18	1420	72	0	14.2	23.2	E
22	1400	39	0	18.5	28.9	F
28	1100	4,710	0	20.8	26.2	------
Apr. 1	1120	3,680	0	19.5	26.9	F
5	1045	86	0	18.2	16.1	F
8	0830	5	0	18.5	25.7	LWS
12	1330	1,000	0	21.0	30.1	F
15	0900	100	0	23.5	28.2	F
19	1115	9	0	22.2	24.1	F
21	1330	50	0	26.0	24.0	HWS
26	1515	56	0	27.0	24.0	F
29	1330	3	0	24.0	23.8	E
May 3	0830	0	0	22.0	22.2	F
6	1400	4	0	24.0	23.0	F
10	0900	6	4	22.2	24.2	E
13	1330	1	1	24.2	29.0	F
17	0845	2	2	24.8	30.5	F
20	0900	9	12	25.6	29.5	F
23	0830	7	82	25.4	27.8	E
26	1545	5	6	29.0	26.9	E
31	1500	0	1	31.2	------	HWS
June 3	1400	0	12	30.7	27.2	LWS
6	1030	0	23	29.0	29.3	F
9	1030	0	0	29.5	32.5	F
14	0830	0	8	28.0	31.2	F
17	0900	167	428	28.4	31.8	E
21	0930	1	6	29.0	32.7	F
24	1515	65	25	28.2	32.5	F
27	1400	108	60	30.0	31.1	F
30	0900	38	98	30.0	26.8	F
July 5	1500	74	148	31.9	31.4	LWS
8	1445	4	1	33.2	25.8	F
12	0930	61	28	30.0	29.4	E
15	1300	30	6	32.0	25.8	E
19	------	18	71	29.0	29.6	F
21	1330	73	35	32.0	31.3	F
25	0940	241	21	30.0	35.5	F
29	1410	8	1	34.0	28.0	E
Aug. 1	------	148	117	29.5	35.6	E
5	1345	21	27	32.0	36.1	F
9	1330	16	24	33.3	34.2	F
12	1430	0	4	29.5	26.3	E
15	1330	257	202	31.0	33.3	E
19	1600	1	2	30.5	27.1	E
22	1000	81	20	28.0	27.8	E
25	0915	306	77	29.5	28.8	LWS
29	1220	8	3	29.0	------	F
Sept. 2	1130	4	9	31.4	26.5	F
6	1400	3	10	32.0	24.6	F
9	1010	0	3	30.1	23.2	E
12	0900	0	1	27.0	25.9	------
16	0930	0	0	27.0	21.3	E
20	0950	1	4	29.0	27.0	E

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°*C.*	o/oo	
1960:—Continued						
Sept. 23	1310	1	2	32.0	27.8	LWS
27	1400	2	5	28.0	24.1	E
30	1615	0	0	30.0	26.5	LWS
Oct. 3	1400	0	0	28.0	28.6	F
7	1100	2	3	27.2	24.6	E
11	1400	0	1	30.0	26.7	E
14	1400	0	2	25.8	28.6	F
17	0845	2	3	25.0	27.0	F
20	0930	0	0	21.0	16.3	E
25	0900	0	0	23.5	27.3	F
28	1415	0	1	27.0	25.5	E
31	1430	0	1	21.3	17.1	E
Nov. 3	1415	1	5	24.0	20.0	F
7	1430	0	0	21.0	22.9	F
10	1600	0	0	12.5	17.9	E
15	1145	1	2	24.0	26.2	F
18	1415	0	0	18.5	26.9	F
21	1630	0	0	18.0	24.9	F
25	1430	1	0	20.0	11.2	E
28	1545	3	1	22.5	24.5	F
Dec. 2	1545	0	0	16.0	27.8	F
6	1530	0	0	19.0	27.1	F
9	1500	1	0	15.5	29.5	F
13	1545	0	0	13.5	31.0	E
16	1445	6	0	13.0	19.2	E
19	1440	0	0	12.0	--------	E
22	1500	0	0	12.2	25.4	E
27	1100	0	0	13.0	19.4	F
29	1145	0	0	12.5	11.1	F
1961						
Jan. 3	1330	0	0	11.8	14.4	E
6	1135	0	0	12.2	24.9	F
10	1530	0	0	13.0	--------	E
13	1405	0	0	12.4	8.3	E
16	1115	0	0	12.5	15.2	E
20	1500	0	0	14.8	7.8	E
25	1410	0	0	10.2	26.8	F
27	1340	0	0	8.0	12.7	E
30	1340	0	0	11.8	11.9	E
Feb. 3	1420	0	0	13.0	13.8	E
7	1430	0	0	11.0	10.8	E
10	1415	0	0	13.0	24.4	F
17	1405	4	0	19.2	28.6	E
21	1420	0	0	15.0	7.6	E
24	1100	0	0	17.0	8.9	E
27	1115	2	0	15.0	10.9	F
Mar. 3	1350	6	0	19.0	30.2	E
6	1510	5	0	19.4	21.8	E
10	1520	2	0	17.8	26.7	E
14	1430	1	0	19.2	26.7	F
17	1400	97	0	20.5	26.7	E
21	1520	28	0	19.7	25.9	E
27	1440	2	0	27.4	25.8	E
31	1040	42	0	20.1	18.2	E
Apr. 5	0845	6	0	19.2	25.3	F
7	1515	12	0	19.5	30.9	E
11	1045	4	0	19.1	29.2	F
17	1555	209	0	20.0	27.8	E
21	1600	10	0	23.0	29.4	E
25	1600	3	0	24.0	25.6	F
28	1550	2	0	24.1	15.0	E
May 2	1355	51	0	25.8	16.6	E
8	1500	889	10	26.9	19.1	E
		—SAMPLING INTERRUPTED—				
Aug. 11	1720	0	0	31.7	30.5	E
15	1410	5	15	33.8	30.3	E
17	0845	6	11	29.8	28.4	E
21	1400	24	10	31.5	20.6	E
24	0915	54	6	29.8	24.6	E
28	1400	8	0	29.8	22.2	F

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°*C.*	o/oo	
1961:—Continued						
Sept. 1	1415	520	544	30.9	21.3	E
6	1415	65	44	33.9	22.3	E
		—HURRICANE CARLA—				
25	1200	5	0	32.0	17.2	F
27	1510	4	0	34.0	17.2	F
Oct. 2	0925	2	1	29.0	18.1	F
5	0900	6	3	20.0	27.8	F
10	1005	32	1	29.0	27.3	E
12	1400	5	0	30.2	24.8	E
16	1545	61	74	24.5	27.4	E
19	1520	6	7	27.0	25.7	E
23	0925	0	0	23.5	24.7	E
25	0905	2	0	24.9	26.3	E
27	0920	144	77	20.5	28.5	E
30	1425	11	3	30.0	29.1	E
Nov. 3	1345	9	4	19.5	27.0	F
6	1520	3	0	12.0	24.0	F
9	0910	45	0	13.0	24.7	E
14	0940	13	1	19.0	23.5	E
16	0945	0	0	17.0	15.0	E
21	0940	1	0	17.5	28.7	F
24	1405	0	0	19.0	28.7	F
27	1020	4	0	21.5	27.5	E
30	0945	0	0	12.0	28.4	LWS
Dec. 5	0930	21	0	20.0	27.5	E
8	1430	0	0	16.0	27.0	F
11	0920	11	0	20.5	25.6	E
14	0920	0	0	8.5	23.1	HWS
19	0925	2	0	13.5	24.4	E
22	1400	1	0	18.0	26.3	E
26	0945	9	0	13.5	27.9	E
29	0920	0	0	10.0	24.4	E
1962:						
Jan. 2	1410	0	0	15.0	27.5	LWS
4	0925	12	0	16.0	31.2	E
9	0925	224	0	12.0	31.0	E
12	0905	5	0	−2.0	30.5	F
15	0905	0	0	6.0	29.9	E
17	1400	0	0	9.0	29.8	F
23	1410	0	0	9.0	27.7	E
26	1045	0	0	15.0	27.2	F
29	0900	0	0	10.0	25.7	LWS
Feb. 1	1550	1	0	14.0	26.5	F
6	0845	73	0	9.0	31.4	E
9	1400	34	0	22.0	29.6	E
12	1030	196	0	19.0	26.3	F
15	1400	48	0	21.0	27.6	F
19	0925	222	0	15.0	27.6	E
23	1340	53	0	22.0	22.3	E
26	0900	1,220	0	22.0	21.7	F
Mar. 1	1525	0	0	5.5	23.0	F
6	1030	40	0	12.0	23.3	E
9	1415	368	0	24.0	24.7	E
12	1100	66	0	17.5	25.5	F
16	1415	8	0	17.5	19.5	F
20	0925	506	0	19.5	26.9	LWS
23	1440	626	0	20.5	26.7	F
26	1035	140	0	19.0	22.3	F
29	1420	75	0	24.0	28.9	F
Apr. 4	0925	1,682	0	16.0	27.0	E
6	1445	234	0	23.0	25.5	E
9	0900	24	0	21.0	24.4	F
12	1445	135	0	24.0	25.3	E
17	0925	192	0	20.5	24.9	E
20	1430	44	0	27.5	24.4	F
23	0905	103	0	24.0	25.2	F
26	1400	3	0	26.0	24.6	F
May 1	1000	4	0	26.0	23.3	E
3	1425	250	0	24.0	18.0	F
7	0910	23	0	24.1	17.7	F
10	0925	7	0	25.0	23.6	F

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrogfaphic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1962:—Continued						
May 15	0925	2	0	26.0	31.7	HWS
18	1500	0	0	27.9	24.2	F
21	0915	0	0	27.0	23.8	F
24	1500	0	0	29.0	24.7	F
29	0905	3	1	26.0	18.9	E
June 1	1430	0	2	26.0	15.7	HWS
4	0925	0	6	26.0	14.7	F
8	1510	6	0	31.5	17.9	HWS
12	0950	8	4	29.5	18.6	E
15	1100	0	0	31.5	26.8	HWS
18	0855	32	6	31.0	26.1	F
21	1423	16	28	34.0	24.4	F
26	0945	0	0	30.5	24.6	F
29	1450	6	6	32.0	23.8	E
July 2	0905	11	13	30.0	23.2	F
5	1100	17	15	33.0	19.9	F
10	0905	0	1	32.0	20.0	E
13	1410	0	0	33.0	31.5	E
16	0845	13	61	30.0	29.8	F
19	1445	48	116	34.0	33.6	E
24	0900	0	1	31.0	35.5	F
27	1410	3	4	32.5	37.4	HWS
30	0910	1	5	30.0	33.8	E
Aug. 2	1415	14	4	33.0	34.4	E
8	0900	19	2	31.0	31.4	E
10	1430	4	4	35.0	35.6	E
13	0905	0	0	30.0	34.4	E
16	1400	145	46	32.0	35.8	F
21	0915	16	29	31.0	36.1	E
24	1405	25	31	33.5	35.6	E
27	0925	76	36	29.0	36.1	E
30	1420	6	29	31.0	29.8	F
Sept. 4	0900	15	106	31.0	30.5	E
7	1410	3	10	31.0	28.6	E
10	0925	25	38	30.5	31.0	E
13	1425	2	2	33.0	31.5	F
18	0905	37	78	30.0	28.7	E
21	1505	11	42	27.0	26.8	E
24	1045	2	7	28.0	25.3	LWS
27	1410	367	1,227	26.0	27.0	F
Oct. 2	1500	24	96	29.0	27.8	F
5	1430	0	6	27.0	26.9	E
8	0920	0	17	29.5	27.0	E
11	1420	0	0	31.0	28.7	F
16	0910	0	1	29.0	30.1	E
19	1440	2	11	29.0	29.8	E
22	0845	6	150	23.0	28.8	LWS
25	1410	4	29	22.0	30.2	F
30	0905	12	46	18.0	26.5	E
Nov. 2	1505	6	13	22.0	29.2	E
5	0845	0	0	17.0	29.1	E
8	1405	1	4	20.0	29.3	E
13	0930	2	0	14.0	30.8	E
16	1445	6	0	22.0	30.9	E
19	0915	0	0	12.0	31.0	F
23	0900	0	0	16.0	29.7	E
26	0905	1	0	18.5	29.9	E
29	1450	0	0	11.0	22.9	F
Dec. 3	0845	13	1	16.5	29.1	E
6	1405	0	0	16.5	20.8	F
11	0915	0	0	16.0	30.6	E
14	1315	0	0	12.0	32.4	LWS
17	0915	0	0	9.0	31.5	F
20	1410	39	0	20.0	31.8	F
26	0905	0	0	11.0	26.3	E
28	1600	0	0	13.0	22.7	F
31	1035	0	0	11.5	28.1	E
1963						
Jan. 4	1445	0	0	15.0	29.1	F
8	0930	1	0	11.0	23.2	E
11	1430	0	0	16.0	31.3	F
14	0845	0	0	0.0	32.4	E

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1963:—Continued						
Jan. 17	1310	0	0	9.0	29.5	F
22	0900	0	0	9.0	24.9	E
25	1430	0	0	7.0	28.5	F
28	0935	0	0	1.0	27.9	E
31	1410	0	0	15.0	25.9	F
Feb. 5	1115	0	0	12.0	29.8	E
7	1435	0	0	16.0	29.6	F
11	0940	0	0	9.0	31.5	E
14	1430	0	0	11.0	25.8	E
19	0935	0	0	8.0	27.2	E
21	1410	0	0	16.0	29.6	F
25	0930	0	0	11.0	28.7	E
28	1415	0	0	15.0	29.7	F
Mar. 5	0920	441	0	14.5	30.4	E
8	1415	16	0	16.0	30.6	F
11	0925	288	0	17.0	30.4	E
14	1400	21	0	18.0	29.0	F
19	0850	280	0	21.0	29.2	HWS
22	1425	286	0	15.0	27.4	E
25	0840	986	0	20.0	26.9	F
28	1350	114	0	27.0	25.9	HWS
Apr. 2	0958	360	0	22.5	27.6	F
5	1146	3,521	0	20.0	27.6	F
8	0925	147	0	21.0	27.6	LWS
11	1415	54	0	28.0	30.6	F
16	0910	167	0	23.8	33.0	F
19	1415	44	0	27.0	32.0	F
22	0910	103	0	25.0	28.0	F
25	1410	93	0	29.0	21.0	E
30	0855	41	3	24.0	21.6	F
May 3	1410	68	5	30.0	20.5	F
6	0910	181	272	25.0	21.7	E
9	1400	71	9	27.0	24.2	F
14	0910	10	0	26.0	28.8	F
17	1410	16	1	29.0	29.0	F
20	0950	17	2	28.0	31.3	E
23	1435	134	70	27.0	34.5	F
28	0915	29	26	27.5	32.3	F
31	1405	28	115	32.0	33.2	F
June 3	0910	381	3,407	34.0	34.8	E
6	1415	5	117	32.0	32.6	E
11	0915	6	19	30.0	30.8	F
15	0915	38	21	28.0	32.9	F
17	1410	7	18	35.0	32.3	F
20	1440	24	10	31.0	33.1	F
25	0915	882	548	29.0	29.9	F
28	1410	211	4	35.0	27.1	F
July 1	0910	16	0	30.0	31.2	F
5	1415	62	9	32.5	31.3	HWS
9	0910	59	29	30.0	31.1	E
12	1415	23	2	31.0	34.3	F
15	0910	33	0	29.0	31.8	F
18	1420	11	2	33.0	34.9	E
23	0910	32	0	31.0	33.6	F
26	1420	23	3	26.0	29.1	LWS
29	0935	14	6	31.0	36.1	E
Aug. 1	1415	7	5	34.0	35.2	E
6	0915	51	21	31.0	34.6	E
9	1415	94	30	33.5	36.5	LWS
12	0915	19	36	29.0	35.0	E
15	1430	27	26	29.5	35.2	E
20	0910	48	12	30.0	35.9	F
23	1415	93	38	35.0	36.9	E
26	0910	4	0	30.0	36.4	E
29	1430	10	5	34.0	37.1	E
Sept. 3	0930	41	28	30.0	37.6	F
6	1430	10	14	29.5	33.3	LWS
9	0910	1	18	30.0	37.1	HWS
12	1410	6	35	32.0	36.7	E
18	0910	24	264	24.0	28.2	F
20	1415	206	132	29.0	27.7	HWS
23	0935	60	94	25.0	27.4	E
26	1420	68	167	26.0	24.9	LWS

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°*C.*	o/oo	
1963:—Continued						
Oct. 1	0910	54	177	21.0	29.3	E
4	1415	4	2	24.0	29.6	LWS
7	0910	19	141	26.0	29.5	E
10	1415	0	47	30.0	30.5	E
15	0910	6	76	26.0	31.4	E
18	1405	14	44	26.5	32.6	F
21	0915	2	14	24.0	31.7	E
24	1415	2	14	26.0	31.8	E
29	0915	10	309	21.0	31.4	HWS
Nov. 1	1505	0	0	19.5	30.7	F
4	0925	4	19	21.0	30.8	E
7	1430	0	0	25.0	30.6	E
12	0925	3	39	18.0	30.0	E
15	1410	0	0	----	30.3	F
18	1505	17	15	26.0	31.3	F
26	1100	0	0	17.0	30.7	F
Dec. 2	1420	0	0	20.0	30.4	E
5	1415	0	0	17.0	32.5	E
10	0950	0	0	15.0	32.8	F
13	1410	0	0	9.0	29.9	F
16	0930	0	0	5.0	31.0	E
19	1430	0	0	9.0	30.3	E
24	1430	0	0	10.0	29.9	E
27	1515	0	0	18.0	31.1	F
30	1005	0	0	10.0	32.8	E

[1] F = Flood; E = Ebb; HWS = High-water slack; LWS = Low-water slack.

TABLE A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960–61*

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°*C.*	o/oo	
1960:							
Apr. 14	C	----	----	----	----	----	----
	D	1200	18	0	21.2	29.8	HWS
	E	1245	137	0	21.5	30.2	HWS
	F	1345	161	0	22.2	30.7	E
27	C	0900	1	0	24.2	23.9	F
	D	0940	3	0	24.7	24.0	F
	E	1030	5	0	25.2	24.2	F
	F	1115	5	0	25.5	23.3	F
May 11	C	1045	0	0	23.2	30.1	LWS
	D	1130	3	0	23.6	30.3	LWS
	E	1230	4	0	23.2	30.8	F
	F	1330	3	1	23.0	31.0	F
25	C	0830	1	4	26.3	29.2	E
	D	0915	11	3	26.8	29.7	E
	E	1000	89	50	27.0	20.8	E
	F	1045	5	14	27.0	29.7	E
June 8	C	0900	2	9	28.0	32.7	F
	D	0945	3	3	29.0	33.1	F
	E	1030	6	2	29.1	33.5	F
	F	1100	2	1	29.0	33.9	F
22	C	0840	191	64	29.6	32.9	E
	D	0940	51	107	30.0	32.9	E
	E	1020	113	122	30.1	33.1	F
	F	1100	28	73	30.8	33.1	F

See footnote at end of table.

TABLE A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960–61*—Continued

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°*C.*	o/oo	
1960:—Continued							
July 6	C	0930	6	11	29.8	31.5	LWS
	D	1000	135	90	30.8	31.9	F
	E	1030	112	168	30.6	31.3	F
	F	1200	125	62	33.0	31.7	F
20	C	0840	39	36	29.4	33.4	E
	D	0920	432	288	29.3	33.4	HWS
	E	1045	392	54	30.0	33.9	E
	F	1200	390	260	30.4	33.3	F
Aug. 3	C	0830	59	63	29.7	36.1	F
	D	0930	97	24	29.8	36.0	F
	E	1000	168	15	30.0	35.9	F
	F	1120	1	0	30.5	35.9	F
16	C	0830	10	10	28.5	----	F
	D	0910	166	14	28.9	32.4	F
	E	1000	897	78	29.2	32.1	F
	F	1130	160	51	30.0	32.2	E
31	C	0840	10	0	29.0	27.5	F
	D	0930	20	13	29.0	29.4	F
	E	1045	28	14	30.2	----	F
	F	1205	65	12	31.2	----	E
Sept. 15	C	0840	6	74	27.8	25.9	F
	D	0935	8	189	28.0	25.5	E
	E	1110	3	12	28.5	25.4	E
	F	1305	2	10	31.3	25.7	E
Sept. 28	C	0845	0	2	24.0	28.1	E
	D	0930	1	1	24.0	28.2	E
	E	1200	0	0	26.0	28.6	E
	F	1040	5	2	25.0	28.6	E
Oct. 12	C	0840	0	0	27.0	28.1	E
	D	0930	1	2	27.4	28.8	E
	E	1030	1	7	27.8	28.9	E
	F	1110	6	5	28.0	29.2	E
26	C	0845	3	4	23.8	27.3	E
	D	0945	2	1	24.4	27.6	E
	E	1040	6	1	24.2	27.2	E
	F	1150	8	4	23.8	26.5	E
Nov. 9	C	1330	1	0	21.3	26.9	E
	D	1110	0	0	21.5	27.5	E
	E	1445	1	0	21.8	27.5	E
	F	1520	0	4	22.0	28.8	E
23	C	1320	0	4	19.5	25.5	E
	D	1405	1	1	20.0	27.3	E
	E	1435	14	11	19.5	25.7	E
	F	1540	6	3	20.0	25.4	F
Dec. 8	C	1405	17	0	17.0	28.2	F
	D	1435	8	0	16.5	28.1	F
	E	1515	18	0	17.0	28.6	F
	F	1600	15	0	16.5	----	F
Dec. 21	C	1355	1	0	10.2	29.3	E
	D	1430	0	0	10.2	29.1	E
	E	1515	0	0	11.0	28.7	E
	F	1545	0	0	12.0	----	E
1961:							
Jan. 4	C	0930	0	0	10.8	27.3	E
	D	1015	0	0	10.9	26.5	E
	E	1100	1	0	11.7	27.3	E
	F	1130	0	0	11.6	26.8	E
18	C	0930	0	0	14.5	27.9	E
	D	1030	3	0	16.0	32.7	F
	E	1115	1	0	16.5	32.9	F
	F	1200	1	0	16.0	32.4	F
Feb. 1	C	1330	0	0	13.0	26.5	E
	D	1420	0	0	13.0	24.6	E
	E	1440	0	0	14.0	24.9	F
	F	1530	0	0	14.0	24.9	F

See footnote at end of table.

Table A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960-61*

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°*C.*	o/oo	
1961:—Continued							
Feb. 20	C	1320	0	0	17.4	26.9	F
	D	1400	2	0	16.9	27.4	F
	E	1435	7	0	17.2	26.9	F
	F	1500	2	0	16.8	26.8	F
Mar. 8	C	1335	14	0	18.0	28.8	E
	D	1415	50	0	16.7	28.8	E
	E	1445	18	0	17.5	29.1	E
	F	1510	138	0	17.9	29.3	E
Mar. 23	C	0900	8	0	17.9	27.2	F
	D	0937	145	0	18.4	27.2	F
	E	1020	72	0	19.0	27.4	F
	F	1037	69	0	19.8	27.4	F
Apr. 5	C	1315	141	0	20.0	29.2	F
	D	1355	217	0	19.7	27.7	F
	E	1425	1,040	0	20.0	30.7	F
	F	1455	2,662	0	------------	33.6	E
20	C	1335	173	0	24.2	29.1	E
	D	1410	254	0	24.0	29.6	E
	E	1430	196	0	23.6	30.4	E
	F	1515	850	0	24.0	31.0	E

[1] F = Flood; F = Ebb; HWS = High-water slack; LWS = Low-water slack.

CODIUM ENTERS MAINE WATERS

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An exotic species of marine algae, *Codium fragile* (Sur.) subsp. *tomentosoides* (Hariot) (fig. 1) was found growing in Boothbay Harbor, Maine, near the Bureau of Commercial Fisheries Biological Laboratory on July 17, 1964. Although the species has been established in the Long Island (N.Y.) and Cape Cod regions for several years, this is its first record from the Atlantic coast north of Cape Cod. In many oyster producing areas, *Codium* grows luxuriantly on the oyster shells and is considered to be a serious pest by the oyster growers.

The specimens from Boothbay Harbor were all collected within 400 m. of the Biological Laboratory in a sheltered cove, and all but one were attached to various objects just below the low tide mark; the single exception was unattached and entangled in some fronds of rockweed (*Ascophyllum nodosum*). Among the substrata to which *Codium* was attached were stones, *Modiolus modiolus* shells, seaweeds, and waterlogged timbers. Because Galtsoff[1] had reported *Codium* from depths down to 12 m., SCUBA divers surveyed the same general area for subtidal specimens. Their survey, as well as littoral surveys in other parts of the harbor, yielded no additional specimens, although more were subsequently found near the site of the original discovery.

Table 1 summarizes the data on all plants collected from July 20, 1964 to August 5, 1965. Gametangia were found on plants only during July and August. Nine specimens bearing gametangia were examined histologically to determine their sex: five bore mostly male, three bore mostly female, and one had about equal numbers of male and female gametangia.

Growth in the Boothbay Harbor area appears to be rapid even during the cold part of the year. For example, plants collected in May 1965 apparently had grown as much as 34 cm. in length since the previous November when they were so small as to be barely visible.

Table 1.—Codium fragile *var.* tomentosoides *collected in the Boothbay Harbor area, 1964–65*

Date collected	Specimens	Length range	Mean length	With gametangia
1964:	*Number*	*Cm.*	*Cm.*	*Number*
July 20	18	9–54	25.6	17
Aug. 11	10	8–20	13.2	7
Sept. 9	7	10–16	13.5	none
Nov. 23	1	20	20.0	Do.
Nov. 24	2	17–20	18.5	Do.
1965:				
May 5	6	11–34	20.3	Do.
July 7	16	3–24	10.6	Do.
Aug. 4	2	13–14	13.5	1
Aug. 5	4	18–43	26.0	4

In the past 60 years, *Codium fragile* appears to have spread widely throughout the world. Silva (1955) presumed its original center of distribution to be the Pacific and Subantarctic regions, perhaps in Japan. It appeared in Holland about 1900 (Van Goor, 1923) and spread to Denmark, Norway, Sweden, England, and France (Silva, 1955). The introduction of *Codium* in Cape Cod was described by Wood (1962), as well as Galtsoff. No certain evidence is available to explain the source of its introduction in Long Island, N.Y., or that of its recent appearance in Maine. One possible explanation of the Maine introduction might be that the

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Note.—Approved for publication April 20, 1966.

[1] P. S. Galtsoff in a manuscript on file at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass., first called attention to *Codium* on Cape Cod in January 1962.

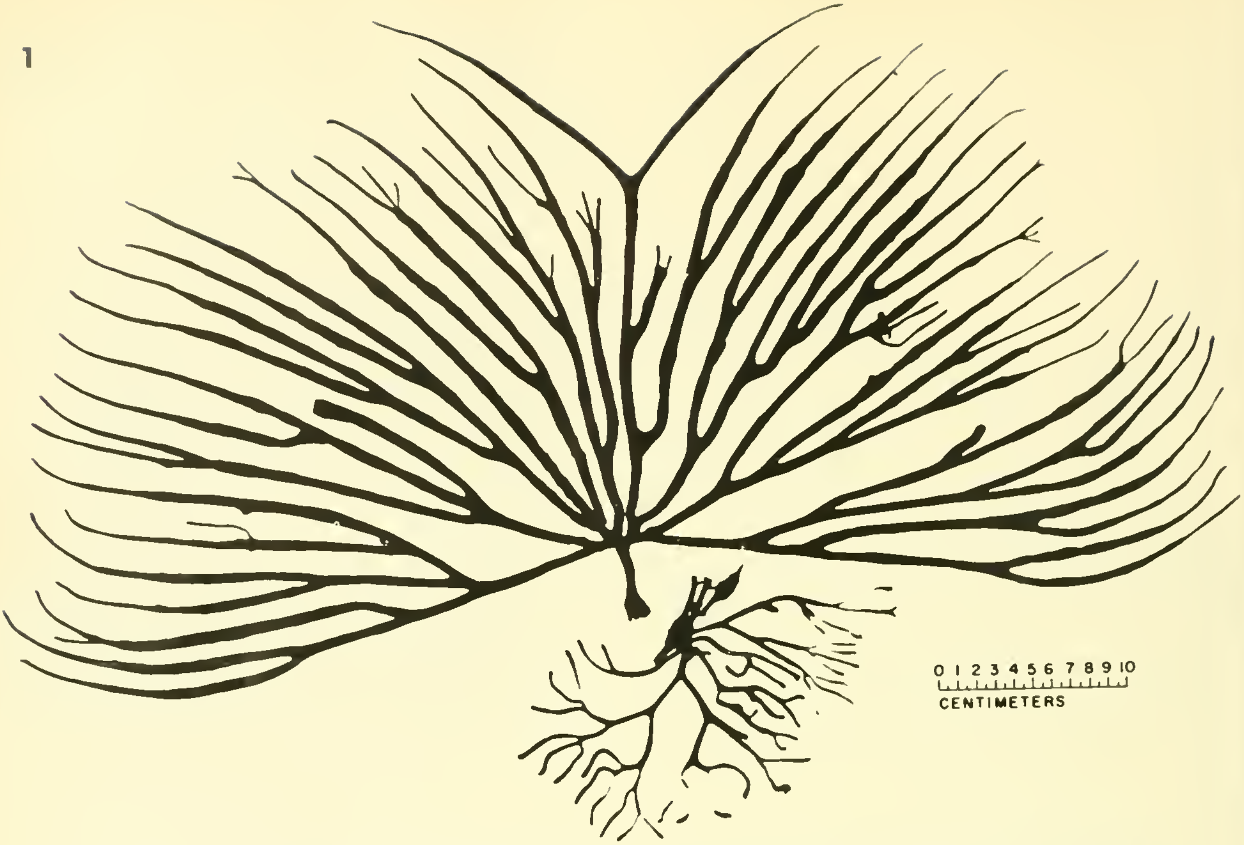

FIGURE 1.—Two typical specimens of *Codium fragile* subsp. *tomentosoides* collected in Boothbay Harbor, Maine.

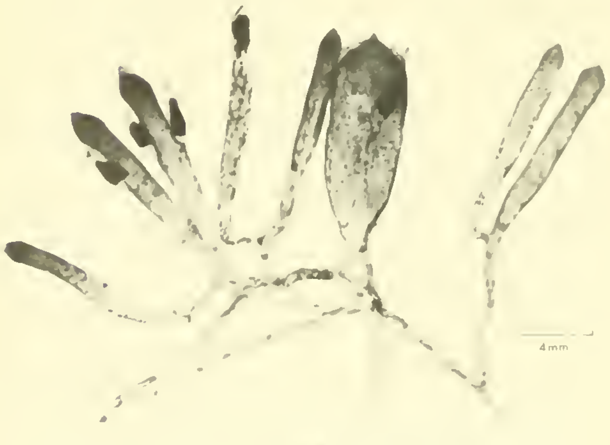

FIGURE 2.—Utricles and attached gametangia from a specimen of *Codium fragile* subsp. *tomentosoides*.

plant arrived on oysters (*Crassostrea virginica*) shipped from Long Island to Boothbay Harbor to delay their spawning by holding them in the colder Maine waters. These oysters were customarily inspected, however, both upon arrival and again before return, to prevent the possible introduction of undesirable species. *Codium* in very early stages of development may have been overlooked when the oysters arrived from Long Island, because at the time *Codium* was not one of the undesirable species being checked; nevertheless, the reexamination before returning the oysters should have brought to light the plants at a larger stage of development.

Codium could possibly have been introduced on the hulls of some of the yachts visiting the area. Such an explanation was not favored by Rosenvinge (1920) who believed the spread in Europe to be due to the breaking loose and drifting of plants or to their being transported along with oysters or other shellfish.

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LABORATORY EVALUATION OF RED-TIDE CONTROL AGENTS[1]

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Intense blooms of the dinoflagellate *Gymnodinium breve* Davis that occur at irregular intervals along the west coast of Florida (Feinstein, Ceurvels, Hutton, and Snoek, 1955) may cause extensive mortality of marine organisms. The blooms are popularly known as red tides because of the amber to red discoloration they impart to the water.

The Fish and Wildlife Service initiated studies in 1948 to determine the possibility of artificial means to reduce the occurrence or intensity, or both, of the red tides. Early tests indicated that copper, in concentrations as low as 0.03 p.p.m., is lethal to laboratory cultures of the red-tide organism. Rounsefell and Evans (1958), and Marvin, Lansford, and Wheeler (1961) demonstrated, however, that control by copper was not feasible under field conditions. The copper precipitated from solution after a few days and, consequently, was ineffective for control.

In 1959, scientists of the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., began a systematic evaluation of 4,306 compounds as red-tide toxicants. The initial phase of the study (Marvin and Proctor, 1964) involved testing each compound to determine its toxicity to *G. breve.* The final phase of the study, described here, evaluated some of the more toxic materials in the laboratory. We investigated only the compounds that we determined to be 100-percent lethal to *G. breve* within 24 hours at concentrations of 0.01 p.p.m. or less. A red-tide control agent must also be selectively toxic; it must kill the red-tide organism without harming other species.

The chemicals fulfilling the toxic requirement for red-tide control were tested for selectivity by determining their effects on juvenile forms of marine species living in Galveston Bay and adjacent coastal waters. The selectivity threshold concentration was set arbitrarily at 0.1 p.p.m. Chemicals that killed 50 percent or more of any test organism within 24 hours at or below this concentration were rejected. The five chemicals that passed the selectivity tests, their effects on the test organisms at the threshold concentration, and the species tested are noted in table 1.

Table 1.—*Percentage mortality of test organisms held 24 hours at toxicant concentration levels of 0.10 p.p.m.*

Chemical	Species[1]							
	Blue crab (megalops)	Striped mullet	Brown shrimp (postlarval)	Sailfin molly	Marsh periwinkle	Sheepshead minnow	Hermit crab	Atlantic croaker
Carbamic acid, diethyldithio-; tellurium salt	0	0	10	10	0	0	0	0
Carbamic acid, dimethyldithio-; ferric salt	10	0	0	0	0	40	0	0
Disulfide, bis(diethylthiocarbamyl)	0	0	10	0	0	0	0	20
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; bis dimethylamino butyne monosalt	10	0	20	0	10	0	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; cyclohexylamine mono salt	0	0	0	20	0	20	0	10

[1] Blue crab, *Callinectes sapidus* Rathbun; Striped mullet, *Mugil cephalus* Linnaeus; Brown shrimp, *Penaeus aztecus* Ives; Sailfin molly, *Mollienesia latipinna* LeSueur; Marsh periwinkle, *Littorina irrorata* Say; Sheepshead minnow, *Cyprinodon variegatus* Lacépède; Hermit crab, *Pagurus* spp.; Atlantic croaker, *Micropogon undulatus* (Linnaeus).

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[1] Contribution No. 215, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.

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TABLE 2.—*Results of six toxicity tests in terms of percentage mortality of* G. breve *after 24 hours exposure*

Chemical	Test numbers for concentration of 0.01 p.p.m.						Test numbers for concentrations of 0.003 p.p.m.					
	1	2	3	4	5	6	1	2	3	4	5	6
Carbamic acid, diethyldithio-; tellurium salt	100	100	100	100	100	100	0	0	0	25	0	0
Carbamic aid, dimethyldithio-; ferric salt	100	100	75	100	100	25	0	0	0	50	0	0
Disulfide, bis(diethylthiocarbamyl)	100	100	75	100	100	0	0	0	0	50	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; bis dimethylamino butyne mono salt	25	100	50	100	75	25	0	0	0	0	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; cyclohexylamine mono salt	25	50	25	100	100	0	0	0	0	0	0	0

The selective chemicals were tested to determine their minimum toxic concentration levels to *G. breve*. Each toxicant was tested six times at 0.01 and 0.003 p.p.m. The results, in terms of mortality of *G. breve*, appear in table 2. Variation was considerable among the supposedly replicate sets of four of the chemicals. This suggests that the concentration of these four chemicals was close to the toxic threshold. At or close to the toxic threshold level, a slight variation in the concentration of a toxicant can have a pronounced effect on the mortality of organisms in cultures containing the toxicant.

Only one of the selective toxicants, carbamic acid, diethyldithio-; tellurium salt, consistently met the toxic requirement arbitrarily established for a control agent (R. T. Vanderbilt Co., Inc., 230 Park Avenue, New York City, N.Y. 10017; $2.13 per pound in 100-pound containers). This compound has two shortcomings, however: it killed 10 percent of the test organisms of two species (table 1); and its cost is prohibitive for massive use in the field.

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OBJECTIVE STUDIES OF SCALES OF COLUMBIA RIVER CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA* (WALBAUM)[1]

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ABSTRACT

This study uses an objective method that measures and graphs the spacings of circuli. It also introduces a new method of differentiating ocean nucleus from stream nucleus. Four groups of chinook salmon scales were studied, each with a specific purpose.

First, scales from recoveries of two kinds of marked fall chinook at Spring Creek National Fish Hatchery were compared: one kind was from fish released as fry, and the other from fish released as fingerlings. In the nuclear part of scale growth, the group released as fry showed a larger variance in spacing of circuli than the group released as fingerlings but the difference in the mean values between these two groups was not significant. In the first marine part of scale growth, circulus spacing was significantly wider in the group released as fry than in the group released as fingerlings. It was not possible, however, to identify individual scales as coming from fish released as fry or as fingerlings.

Second, scales from marked and unmarked fall chinook salmon at Spring Creek Hatchery were compared to see if any effect of marking could be detected. Significant differences in circulus spacing in marine growth existed between marked and unmarked fish, the latter having wider spacings. Marking was in the removal of adipose and right pectoral fins from chinook fingerlings. This technique was therefore regarded as having unfavorably affected the growth of marked fish.

Third, scales from marked fall chinook that had been released at various times of the year at Little White Salmon National Fish Hatchery were studied. The scales showed that young chinook salmon released in May and July of the first year grew an ocean nucleus typical of fall chinook; those released in February of the second year grew a stream nucleus typical of spring chinook; and those released in September and October of the first year grew a nucleus intermediate in character.

Fourth, scales of fall and spring chinook salmon were studied to see how these two groups could be identified by their scales. Measurements of circulus spacing in the first and second summer of marine growth revealed that, in the spring chinook, marine circuli in both summers were about equally wide; whereas, in the fall chinook, marine circuli of the second summer were nearly one and one-half times wider than those of the first summer. Thus, these scales can be distinguished, not by nuclear growth as is normally done by subjective judgment, but by relative marine growth as measured by objective means.

Since the early studies on the scales of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), by Gilbert (1914), Rich (1922), Rich and Holmes (1929), and others, little has been published on the subject. Many problems still deserve further study. The most important and interesting problem is the classification and identification of nuclear growth zones, the central part of scale growth. Gilbert (1914) classifies chinook scales into two types: those with an ocean nucleus and those with a stream nucleus. The ocean nucleus type originates from fish that migrate seaward in their first year and thus has the first annulus at the end of the first year's marine growth; the stream nucleus type originates from fish that do not migrate seaward until the early months of the second year and thus has the first annulus at the end of fresh-water growth. To the former group belongs the fall run of chinook, which enters the river from July through November; to the latter, the spring run, which enters the river from March to June.

Classification of nuclear growth zones is very useful and today still serves as the foundation of age study of chinook salmon. This method is most useful when only two groups of chinook salmon are involved and their nuclear zones

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are clearly defined. Its application becomes limited, however, when the boundaries of nuclear growth are not clear-cut. The chinook salmon young of the Columbia River, for instance, migrate seaward throughout most of the year (Rich, 1922); consequently, the first year's growth is subject to numerous variations that intergrade so completely that it is impossible to draw any sharp line of distinction (Rich and Holmes, 1929). Most Columbia River chinooks, according to Rich and Holmes (1929), have neither typical stream nor typical ocean nuclei, but apparently have spent part of the first year in fresh water and part in the ocean. The result has been a nuclear area composed in part of stream growth with narrowly spaced circuli and in part of ocean growth with widely spaced circuli to form what these authors term "composite nucleus."

The composite nucleus makes age determination difficult. In a composite nucleus, the amount of stream growth varies inversely with the amount of ocean growth. At one extreme is the type with only a small amount of stream growth accompanied by a large amount of ocean growth. At the other extreme is the type with a great amount of stream growth accompanied by a small amount of ocean growth. The first type of nuclear growth approaches the ocean nucleus, and the second type approaches the stream nucleus. Between these two extremes there are complete intergradations. This poses the question: "Where should the annuli be placed, and how many?"

The question is further complicated by the formation of the so-called "intermediate growth," that is, growth of circuli in the estuary while the fish is migrating seaward. Circuli of this growth cannot be distinguished with certainty from either the stream or the ocean circuli, and they often form a check which, in the words of Rich and Holmes, "might easily be mistaken for an annulus by an inexperienced observer." These same authors maintain that with experience this kind of error may be eliminated almost completely, and that their own experience with the scales of fish of known history has provided sufficient information for correct age determination.

The prerequisite of experience in scale reading cannot be denied, but the dependence upon experience can be lessened and the accuracy of age determination improved if some mechanical method in scale work can be developed so that the scale growth and marks can be interpreted more objectively. The development of an objective method is the major purpose of the present work. From a large number of scales collected from chinook salmon of known ages through recoveries of marked fish, we were able to establish some definite criteria and methods whereby one can objectively interpret scale marks with a minimum amount of guess work.

The present study comprises four parts. First, scales from adult fall chinook that have migrated seaward as unfed fry and as fed fingerlings [1] were compared in an attempt to find characteristics that might serve to identify fish of unknown origin; i.e., whether they come from fry migrants or from fingerling migrants.

Second, comparative studies were made between scales from fall chinook that had been fin-clipped when released as fingerlings and those that had not been marked. This was to see if marking had any adverse effect on growth that could be detected by scale measurements.

Third, marking experiments on young fall chinook performed by U.S. Fish and Wildlife Service personnel at the Little White Salmon Hatchery provided an unusually valuable series of adult scale samples for age and growth study. Young chinook salmon were released over a wide range of time (May to February), and each release had a different mark. Scales from returned adults originating from different releases were studied to gain insight into the formation of a fresh-water annulus and to assess the relative amount of first and second year's ocean growth due to different release dates. This provided valuable information for understanding scale growth patterns in fall and spring chinooks.

Fourth, the relative amount of the first and second year's ocean growth on scales in known stocks of fall and spring chinooks was studied and compared. An objective method of determining the presence or absence of an annulus in nuclear growth and therefore in distinguishing fall and spring chinooks was developed, independent of fresh-water growth itself.

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[1] "Fed fingerlings" refers to young chinook salmon that have been fed for about 3 months.

MATERIALS AND METHODS

Materials for the present study were supplied by the Fish Commission of Oregon and by the Portland Program Office of the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. Scale impressions on cellulose acetate cards of the following were available for study.

1. Returns of marked fall chinook to Spring Creek Hatchery:
    a. 1958 returns—released as fry, 1 fish; released as fingerlings, 8 fish.
    b. 1959 returns—released as fry, 8 fish; released as fingerlings, 173 fish.
    c. 1960 returns—released as fry, 28 fish; released as fingerlings, 158 fish.
2. Returns of unmarked fall chinook to Spring Creek Hatchery:
    a. 1959 returns—925 fish.
    b. 1960 returns—898 fish.
3. Returns of marked fall chinook to Little White Salmon Hatchery:

Mark*	Date released	*Fish returns in 1959*			*Fish returns in 1960*		
		Male	Female	Total	Male	Female	Total
		No.	*No.*	*No.*	*No.*	*No.*	*No.*
LP	—May 8-9 (1957, 1958)	10	3	13	12	6	18
RP	—July 1-2 (1957, 1958)	27	6	33	28	18	46
D-LP	—Sept. 4 (1957, 1958)	3	....	3	4	2	6
D-RP	—Oct. 15 (1957, 1958)	6	1	7	2	2	4
An-RP	—Oct. 15 (1957, 1958)	20	....	20	20	11	31
An-LP	—Feb. 13-15 (1958, 1959)	43	10	53	48	24	72
Total	....	109	20	129	114	63	177

*L=left; P=pectoral; R=right; D=dorsal; An=anal.

4. Returns of unmarked spring chinook to Carson National Fish Hatchery: Samples of several hundred scales (one from each fish) each year collected during 1955–57 and 1959–60.

In addition to the above impressions of scales of adult chinooks, specimens of young fall chinook, preserved at the time of release at several Federal hatcheries, were also available. Scales from these young fish were studied for comparison with the nuclear zone of adult scales.

The study was based on objective means as much as possible. Scales were studied under a microprojector at magnifications of 92, 140, or 400 times, depending on the magnification desired. The image of a scale was projected directly on millimeter graph paper, and the positions of circuli along the antero-lateral radius of the scale were marked on the paper. The center of the central plate was always used as the starting point, and the edge of the central plate became the first mark. In counting and measuring the circuli, we regarded the mark next to the central plate as the first circulus.

All subsequent studies of the scale growth were made from the markings on the graph paper. Distances were measured in terms of millimeters, and the actual dimensions determined by the magnifications used. The various methods of counting, measuring, and graphing will be described under individual sections.

SCALE GROWTH IN FALL CHINOOK SALMON RELEASED AS FRY AND FINGERLINGS

Spring Creek Hatchery (fig. 1), a Federal installation located about 175 miles from the mouth of the Columbia River on the Washington side, produces primarily fall chinook salmon. In the past, young chinooks were released either as unfed fry during the first week of February or as fed fingerlings during the first week of May. To evaluate the relative merits of fry and fingerling releases, the Bureau of Commercial Fisheries marked young chinook salmon of brood years 1956, 1957, and 1958. Among the young released each year during 1957–59, some fish were marked, consisting of about equal numbers of fry and fingerlings. Two combinations of fin marks were used: adipose and left pectoral fins on fry and adipose and right pectoral on fingerlings.

Fish with both marks were recovered in years 1958–60,[5] and scales were collected from all returned fish. An interesting question here is: "Can the scales of adults that were released as fry be differentiated from those that were released as fingerlings?" This problem is of both theoretical and practical importance.

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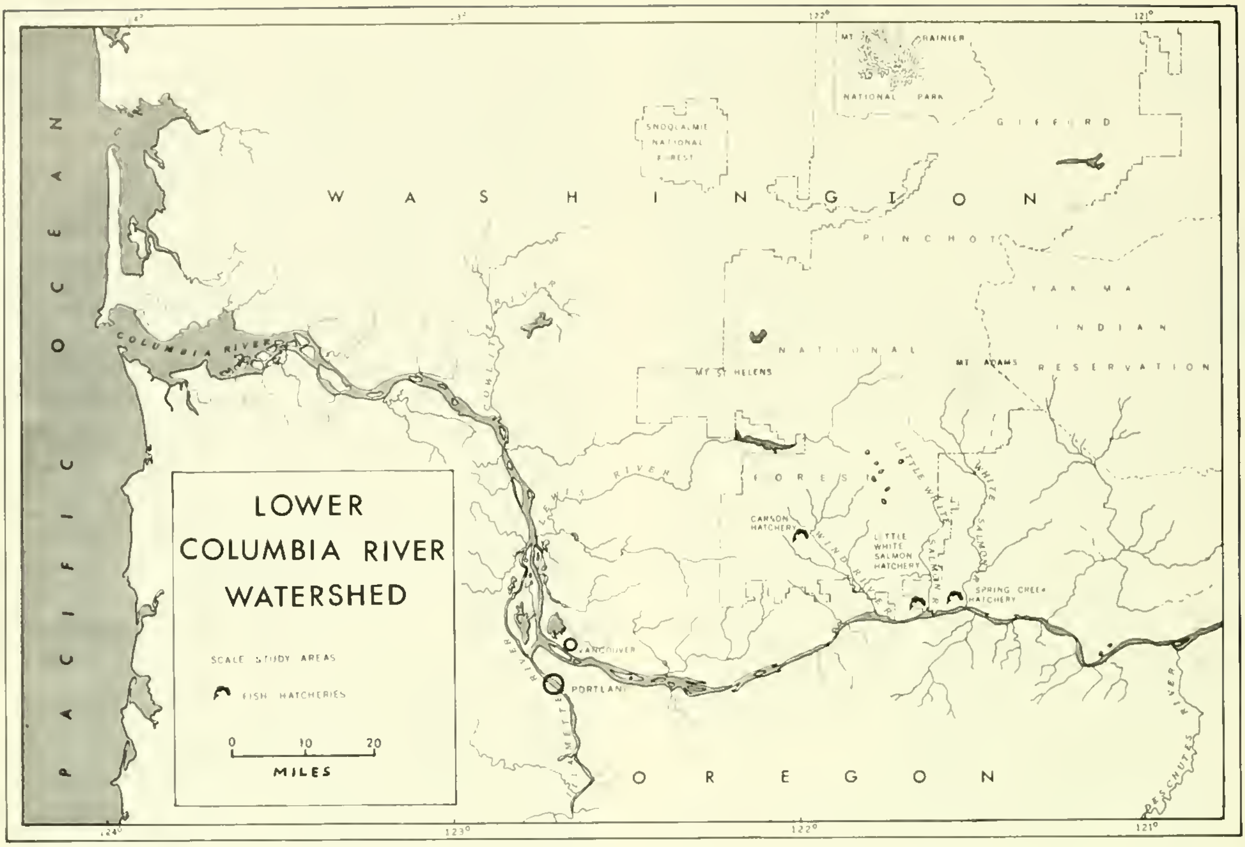
[5] Later recoveries are not included in the present study.


LOWER COLUMBIA RIVER WATERSHED
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SNOQUALMIE NATIONAL FOREST
GIFFORD PINCHOT NATIONAL FOREST
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MT ST HELENS
MT ADAMS
COLUMBIA RIVER
COWLITZ RIVER
LEWIS RIVER
WIND RIVER
LITTLE WHITE SALMON R
WHITE SALMON
WILLAMETTE RIVER
DESCHUTES RIVER
CARSON HATCHERY
LITTLE WHITE SALMON HATCHERY
SPRING CREEK HATCHERY
VANCOUVER
PORTLAND
124°
123°
122°
121°

FIGURE 1.—Map of lower Columbia River watershed, showing locations of the three National Fish Hatcheries from which study materials were obtained.

Theoretically speaking, these two groups of fish should have differences in the growth pattern of scales, because at the time of release the fry have not started to grow scales, whereas the fingerlings have already grown scales with circuli. The nuclear area (the central portion of the scale), or at least the initial part of it, of adult scales originating from these two groups of fish must have then grown under different conditions: that from the fry group in river water under lower but variable temperature[6] and feeding conditions, and that from the fingerling group in hatchery water with higher and nearly constant temperature[7] and ample food. It may be expected then that scales from fish released as fry should have more closely spaced circuli in the nuclear zone than those released as fingerlings. Further, because the fry were released 3 months before the fingerlings, they should reach the ocean earlier and consequently may have a different pattern of ocean growth than have the fingerlings.

Practically speaking, if the origin of release — whether fry or fingerling — of returning adults can be identified through scale characters, then the two methods of release can be evaluated without having to mark young fish. Junge and Phinney (1963) indicate that fish released as fingerlings have a much greater survival rate than have fish released as fry. Therefore, the elimination of marking would not only save the costs of marking but also eliminate any possible harm that marking may cause the fish.

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[6] Water temperatures of Columbia River at Bonneville Dam in February were 2.8–4.4°C. (1957); 6.1–8.3°C. (1958); 3.9–5.0°C. (1959). U.S. Army Corps of Engineers, Annual Fish Passage Reports.

[7] Water temperature in Spring Creek Hatchery is about 7.8°C. year-round.

To find out whether actual differences existed between scales of adult fish released as fry and those from adults released as fingerlings, we selected scale samples from brood year 1956 because that year had the largest number of specimens that were released as fry. Returns of fish released as fingerlings are plentiful for analyzing this group in any brood year.

In 1959, eight fall chinook salmon with Ad–LP mark (released as fry) were recaptured. Of these, seven were 3 years old and therefore came from 1956 brood. In 1960, 28 such marked chinooks were recaptured and 16 of these were 4 years old and of the 1956 brood. This total of 23 scales that belonged to the 1956 brood, plus 102 3-year-olds that were recaptured in 1959 with Ad–RP marks (released as fingerlings) and 167 4-year-olds that were recaptured in 1960 with the same mark, provide the samples for the following study.

Based on theoretical considerations given earlier, we used two purely objective methods aimed at detecting any difference these two groups of scales might have in growth in fresh water or the first year of growth in the sea.

The first objective method was that of comparing growth patterns revealed by scale graphs based on spacing of circuli. Under a magnification of 140 times, the circuli were marked along the antero-lateral radius on a millimeter graph paper. We then divided the radius into 20-mm. units and calculated the mean spacing of circuli of each unit. For each group of scales, the means of circulus spacing of a unit were summed and averaged to give the mean of the group. When the group means were plotted on the ordinate against the radius units on the abscissa, we obtained a scale graph which shows the growth pattern.

Figure 2 shows information on groups released as fry and as fingerlings.

The fresh-water growth part of figure 2 shows a similar pattern for the two groups, namely, circuli are wide at the start but rapidly narrow down; the extent of growth covers about the same distance on scale radius. Also, there is only a slight difference in the mean spacing of circuli. Such difference, as will be shown in the second method, is not statistically significant.

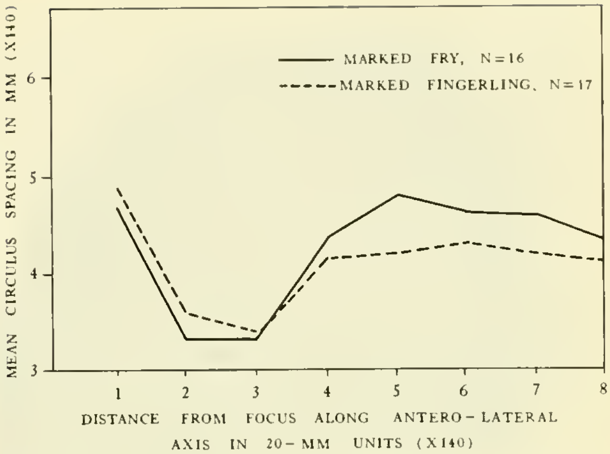

FIGURE 2

Figure 2.—Spring Creek Hatchery chinook salmon: Mean scale graphs showing pattern of fresh-water growth and the major portion of first year's marine growth of group marked as fry (solid line) and of group marked as fingerlings (dash line).

Marked difference, however, is evident in the marine growth section of figure 2 (units 4 to 8). The group released as fry has much wider circuli at every unit than has the group released as fingerlings. This is, of course, only a reflection of group difference, as the values plotted are mean widths. At each unit, the mean circulus widths of the two groups of scales overlap widely so that we could not identify the group origin of individual scales on that basis. Examples of scales of adults that were released as marked fry and as marked fingerlings are shown in figures 3 and 4.

The second objective method, aimed at detecting differences in first year growth of fish released as fry and as fingerlings, was to measure and compare the total distance of the first 5 circuli, of the first 10 circuli, and of 10 circuli counted from the 16th through 25th circulus.

The reasons for the selection of these three measurements are as follows: Fish released as fingerlings have developed, in the hatchery, the first 5 circuli and most, if not all, of the first 10 circuli; but the fry that are released develop all circuli in the natural environment. We measured the first 5 and first 10 circuli, therefore, to detect differences in initial fresh-water growth. The third measurement, distance from the 16th through 25th circulus, was made to

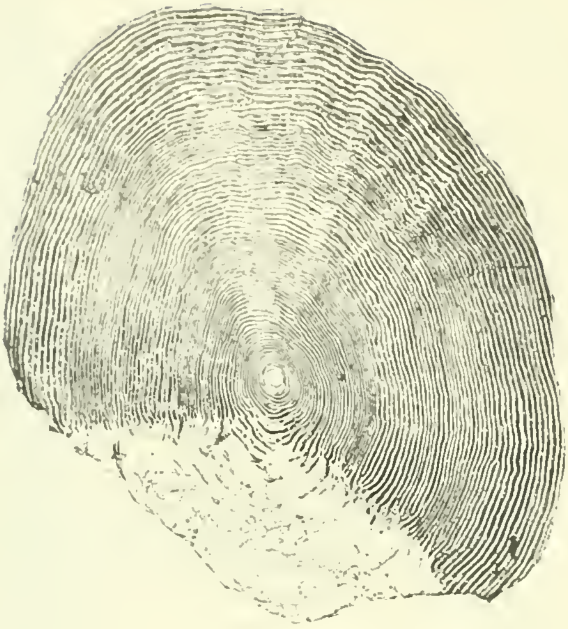

FIGURE 3.—A scale of Spring Creek Hatchery chinook salmon that was released as marked fry. Note the relatively wider spacing between circuli in the first year of marineg rowth.

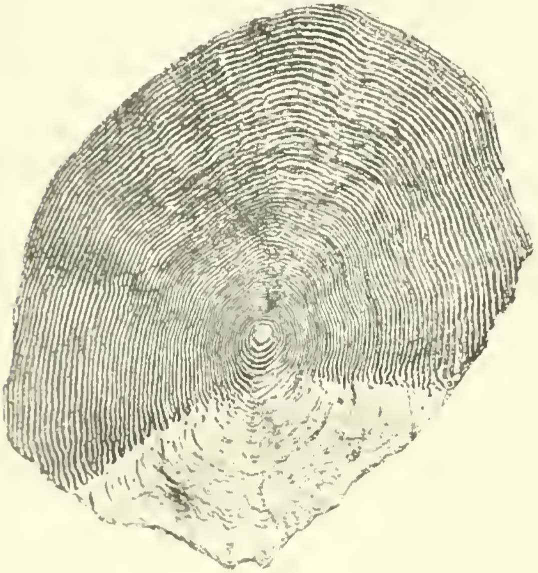

FIGURE 4.—A scale of Spring Creek Hatchery chinook salmon that was released as a marked fingerling. Note the relatively narrower spacing between circuli in the first year of marineg rowth.

study first-year marine growth, because these 10 circuli always represent the major but not the entire part of the first summer growth in the ocean. Using the 10 circuli enables us to have more consistent measurements than we would obtain by measuring the entire first summer growth, because we cannot delimit exactly the first and last circuli of summer growth. Circuli 11 through 15 were purposely skipped, for they may represent some transitional growth and therefore are quite variable as a group.

In reference to scale graphs, the initial 10 circuli are represented by the first two and a half units on the abscissa; and circuli 16 to 25, by units 4 to 6. In essence, the measuring method enables us to check on the graphing method, for we can tabulate the data and subject the results to statistical tests.

The results of the measurements and statistical tests are shown in table 1. In all the tests between the paired sample means, we first tested for the variances (s^2) and then applied the appropriate t-test.

In the comparisons of the first 5 circuli and of the first 10 circuli, the variances of the paired samples are significantly different, and t-test shows that the sample means are not significantly different. This is to say that although circulus spacing in the initial 5 or 10 circuli is more variable in the group released as fry (larger variance) than in the group released as fingerlings, the average values do not differ significantly between these two groups. The latter point confirms the results of the scale graph method

In the comparison of the 10 circuli counted from 16th to 25th circulus, the variances are not significantly different, and t-test shows that the sample mean of "A" (fry releases) is significantly larger than that of "B" (fingerling releases). This is to say that the groups released as fry and as fingerlings have a similar amount of variation in circulus spacing for circuli 16 to 25, but that the average spacing of circuli in the group released as fry is larger than that in the group released as fingerlings. The latter point also confirms the results of the scale graph method.

TABLE 1.—*Frequency and statistics of total distance of circuli of two groups of scales from salmon returning to Spring Creek Hatchery: A—adult chinooks that were marked and released as fry; B—adult chinooks that were marked and released as fingerlings*

Distance	First 5 circuli		First 10 circuli		Circuli 16–25	
	A	B	A	B	A	B
Mm. x 140	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
12–14		2				
14–16	6	12				
16–18	5	66				
18–20	6	70				
20–22	0	74				
22–24	4	31	1			
24–26	1	10		1		2
26–28	1	3		3		1
28–30		1	4	14	1	9
30–32			4	22	1	13
32–34			5	47	2	36
34–36			2	57	1	41
36–38			1	47	5	45
38–40			1	43	3	36
40–42			2	22	1	35
42–44			1	7	3	24
44–46			2	4	2	14
46–48				1	3	10
48–50				1		
50–52					1	2
52–54						
54–56						1
N	23	269	23	269	23	269
$\bar{x}$	18.8	19.6	34.3	35.8	39.8	37.7
s^2	12.69	6.94	32.58	14.97	32.63	23.12
95% confidence limits for ratio of population variances.	$1.09<\frac{s_A^2}{s_B^2}<3.66$		$1.31<\frac{s_A^2}{s_B^2}<4.36$		$0.84<\frac{s_A^2}{s_B^2}<2.82$	
t-statistic	−1.05		−1.24		2.10*	
d.f.	53		24		290	
Value of $\|t\|$ at 0.05 significance level.	2.01		2.06		1.96	
95% confidence limits for difference between population means.	$-2.34<\mu_1-\mu_2<0.74$		$-3.99<\mu_1-\mu_2<0.99$		$0.14<\mu_1-\mu_2<4.01$	

That the variances of circulus spacing in both the first 5 circuli and the first 10 circuli are significantly greater for the fry-released group than for the fingerling-released group is as we expected, because the fry group grows the first 5 to 10 circuli in the river or estuary, where food and temperature conditions can be highly variable, while the fingerling group grows these same circuli in the hatchery, where the conditions are fairly uniform. Both groups form circuli 16 to 25 in the ocean, which explains why there is no significant difference between the two variances. Why the group released as fry grows more widely spaced circuli than does the group released as fingerlings is not understood. Perhaps it is due to the earlier entry into the ocean by the fry.

SCALE GROWTH IN MARKED AND UNMARKED FALL CHINOOK SALMON

During the 3 years 1957–59 when the Bureau of Commercial Fisheries marked the fall chinook salmon at the Spring Creek Hatchery, both marked and unmarked fish were released simultaneously. When the fish returned, the unmarked fish had a much greater rate of return than the marked fish. Also, at the same age the unmarked chinook were consistently larger than the marked. Examples are given in figure 5 in which the modal length of female unmarked fish is 2 inches, or 6 percent, larger than that of female marked fish, which had their adipose and right pectoral removed. Male chinook salmon exhibited similar differences.

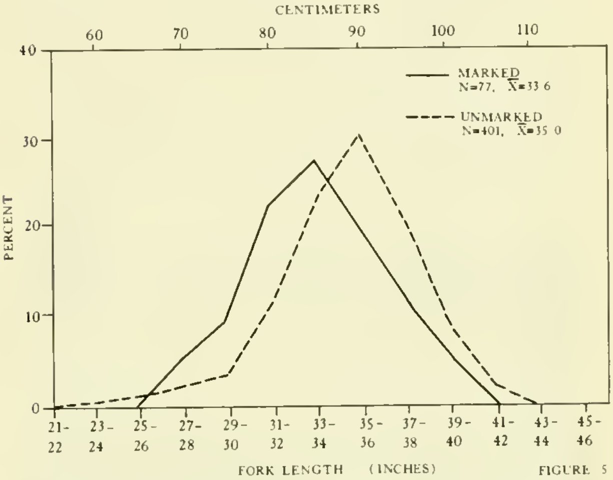

FIGURE 5.—Size frequencies of female 4-year-old Spring Creek Hatchery marked and unmarked chinooks that were released as fingerlings (1956 brood) returned in 1960.

To see if the difference in size between returns of marked and unmarked chinook is manifested in scale growth, we studied the returns of 4-year-old females in 1960. We first compared scales from fish of modal length in each group (33–34 inches in the marked group and 35–36 inches in the unmarked group). Then, we studied unmarked fish 33 to 34 inches long. To do this objectively, we constructed and compared mean scale graphs showing circulus spacing and growth pattern. Of the marked fish returns, only the group released as fingerlings were studied for very few returns were available from fish released as fry.

The three mean scale graphs for the marked and unmarked female fall chinook salmon that returned to the Spring Creek Hatchery in 1960 as 4-year-olds are shown in figure 6. These graphs show the growth period from the beginning of scale growth toward the end of the first summer in the ocean. They represent, therefore, only part of the antero-lateral radius. The initial part of the graphs (units 1–4), which represents fresh-water and intermediate growth, is very similar among the three groups. The remaining part of the graphs (units 5–8), which represents the major part of first marine growth, becomes divergent in that the mean circulus spacing of the marked group is consistently smaller than that of either of the two unmarked groups (33–34 inches, 35–36 inches), with greater difference shown between the marked and the larger unmarked fish.

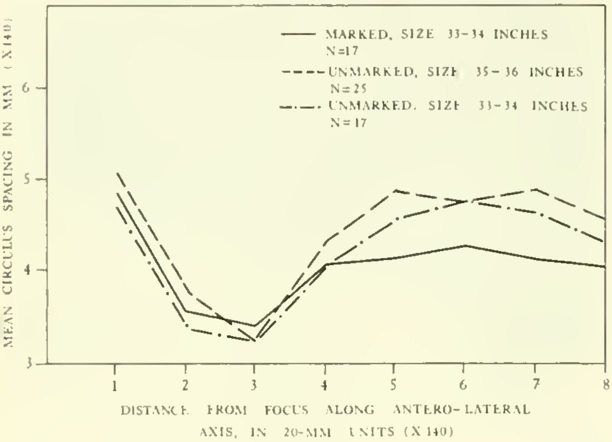

FIGURE 6

FIGURE 6.—Mean scale graphs of marked and unmarked female fall chinooks of three selected size groups that returned to Spring Creek Hatchery in 1960 as 4-year-old fish.

The fact that the initial part of the scale graphs is similar among the three groups of chinook salmon is easily understood, because marking is applied during the fingerling stage after the fish have grown the initial part of the scale. The difference in the remaining part of the scale graphs between the marked and unmarked groups, especially between those of the same size, strongly suggests that marking has slowed down the fish's growth rate, at least during the first summer in the ocean.

To verify the results revealed by the scale graphs, the total distance from the 16th to 25th circulus, which represents the major part of the first year's marine growth, was measured and a *t*-test applied (table 2). We first tested sample variances, and in both pairs equality can be accepted; therefore, a simple *t*-test was used. The width of ten marine circuli was significantly greater in the unmarked groups than in the marked group, compared either between two modal lengths of fish or between fish of the same length. These tests thus confirm the results obtained by the scale graph method.

TABLE 2.—*Frequency and statistics of measurements of scale growth during first year's marine life in marked and unmarked fall chinook salmon that returned in 1960 to Spring Creek Hatchery as 4-year-olds*

Distance of 10 circuli (16th–25th)	Marked fish 33–34 inches long	Unmarked fish 33–34 inches long	Marked fish 33–34 inches long	Unmarked fish 35–36 inches long
	A	B	A	B
Mm. x 140	*Number*	*Number*	*Number*	*Number*
31	1		1	
32	0		0	
33	0		0	
34	1		1	
35	0		0	
36	1	1	1	
37	2	0	2	
38	2	0	2	1
39	1	0	1	0
40	0	2	0	0
41	2	1	2	4
42	0	1	0	0
43	1	1	1	2
44	3	2	3	1
45	0	2	0	2
46	1	0	1	0
47	0	1	0	3
48	0	0	0	1
49	0	0	0	1
50	0	2	0	4
51	2	2	2	1
52		2		3
53				1
54				1
55				1
N	17	17	17	26
$\bar{x}$	40.88	45.47	40.88	47.27
s^2	30.23	23.89	30.23	22.12
95 percent confidence limits for ratio of population variances.	$0.29 < \frac{s_A^2}{s_B^2} < 2.19$		$0.28 < \frac{s_A^2}{s_B^2} < 1.74$	
t-statistic	−3.58*		4 12*	
d.f.	32		41	
Value of [*t*] at 0.05 significance level.	2.04		2.02	
95 percent confidence limits for difference between population means.	$-9.95 < \mu_1 - \mu_2 < -2.73$		$3.25 < \mu_1 - \mu_2 < 9.53$	

Growth rates of fishes are reflected in the spacing of scale circuli: the faster the growth rate, the wider the spacing between circuli. The present findings, therefore, suggest that marking through the excision of adipose and right pectoral fins in chinook salmon may have been responsible for the slower growth rate of the marked fish. Biologists, using various fin marks, working on various species of fish, and experimenting under various conditions, have obtained contradictory results in this respect. Ricker (1949), for instance, excised the pectoral, both ventrals, or one pectoral and both ventrals of the largemouth bass and found that recoveries of these and unmarked fish indicated that the marked fish were significantly smaller than the unmarked ones. He believes that marking possibly affected the growth rate directly; however, when he marked 2-year-old bluegills, the growth of marked and unmarked fish was the same. Armstrong (1949) studied lake trout fingerlings and found no appreciable difference in length and weight between those that were unmarked and those that had had the adipose removed. Shetter (1951) also shows that removal of the dorsal and adipose fins, right pectoral fin, or right pelvic fin from the fingerling lake trout had no effect on the growth of the marked fish but that removal of the left pectoral appeared to have slowed the growth of the fish. Again, on a study of growth of marked and unmarked lake trout fingerlings in the presence of predatory fish, Shetter (1952) found no significant difference in the growth rate between marked and unmarked groups.

In the Cultus Lake experiments on the sockeye salmon, Foerster (1934, 1936a, 1936b) shows that unmarked smolts had a return rate two and one-half times greater than marked smolts that had both pelvics and adipose or both pelvics and dorsal removed. He shows further that this differential mortality was due to the effect of marking upon marine survival, since marking did not affect lake survival. No data on fish length or scale growth were given, however, so it is not known whether marking did have an adverse effect on growth.

The reasons for the apparent paradoxical results on the effect of marking on the growth rate of fish by various workers may be quite varied. The different results could be due to different fins being clipped, different species being experimented on, different techniques being applied, or different conditions under which the experiments were made.

SCALE GROWTH OF FALL CHINOOK SALMON, RELEASED BETWEEN MAY AND FEBRUARY

At Little White Salmon Hatchery (fig. 1), another Federal installation some 10 miles downriver from the Spring Creek Hatchery, the Bureau of Commercial Fisheries has conducted further marking experiments on fall chinook salmon. Here, for the brood years 1956–58, young chinook salmon were reared for various lengths of time and released at five different times of the year from May to February (see under "Materials and Methods"). A different mark was applied for each release, so that at return a marked fish could be positively identified as to its date of release.

The returns from these experiments offer excellent scale samples for studying the growth of nuclear zones. Fish released earliest (May) should go to sea during the first year, and their scales should show a typical ocean nucleus. Those released latest (February of the following year) spent the first winter in the hatchery, and their scales should therefore have a stream nucleus. Fish released between the above pe-

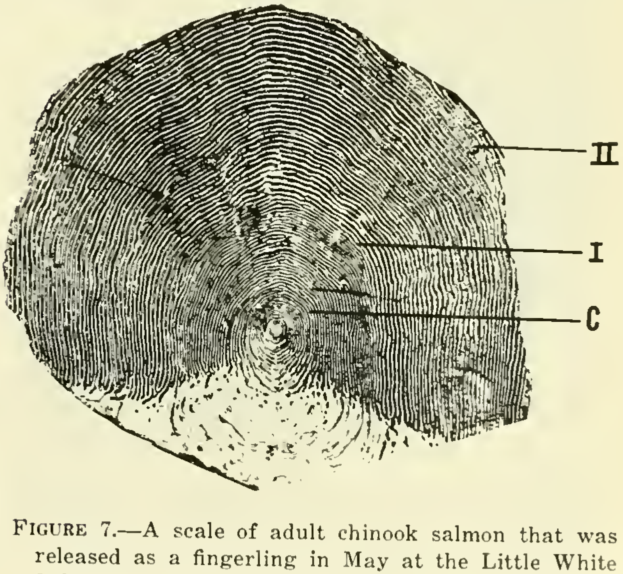

FIGURE 7.—A scale of adult chinook salmon that was released as a fingerling in May at the Little White Salmon Hatchery (May 1957 release, 1959 return).

riods (July, September, and October) should have scale growth of intermediate nature.

First, let us examine a typical scale of an adult chinook that originated from May release (fig. 7). At the center of the scale, there are 14 closely placed fine circuli, which are followed by more widely spaced coarser circuli. A check-like structure (C) is present at the border between the two zones. Most of the fine circuli represent intermediate growth that took place after the fish was released, because young chinook released in May average only two to three circuli on their scales. The zone of more widely spaced coarser circuli that follows the check represents what is generally regarded as marine growth. It is bounded by a distinct band of closely placed circuli (fig. 7, I). Both the check (C) and the band (I) have the appearance of an annulus. But since this is known to be an age II fish (1957 release, 1959 returns), and since the second annulus (II) is evident near the resorbed margin of the scale, only one of the two marks can be regarded as a genuine annulus. Based on relative distance, the band (I) should be regarded as the first annulus. "C," therefore, is a sort of migration check. The entire growth up to and including the band (I), forms what is known as the ocean nucleus. In the ocean nucleus, then, an annulus in the fresh-water growth part is lacking, and that gives rise to the age terminology of "sub-one" for this group,[8] or "O.", to use the terminology of Koo (1962).

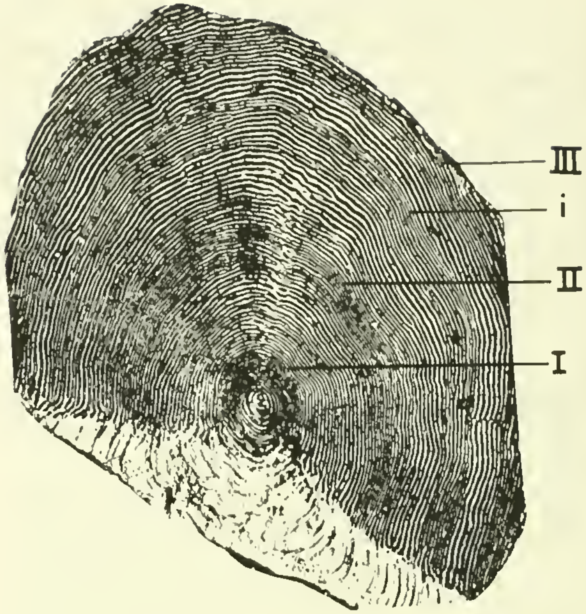

FIGURE 8.—A scale of adult chinook salmon that was released as a fingerling in February at the Little White Salmon Hatchery (February 1958 release, 1960 return).

Next, let us examine a tipical scale of an adult chinook that returned in 1960 from a February 1958 release (fig. 8). Here, there is also the central crowded area of fine circuli (I) and the surrounding wide marine growth that is bounded by a band of closely placed narrow circuli (II). Although "I" and "II" in this figure appear to be corresponding respectively to "C" and "I" in figure 7, they are different in significance. Because the fish was held in the hatchery over the winter and was not released until February, "I" in figure 8 is a true annulus, not a mere check, as the "C" in figure 7. The central area up to "I" forms what is known as the stream nucleus and because the young fish left fresh water during its second year, it is also referred to as "sub-two age," or "1.", meaning one annulus in fresh-water growth. This fish is known to be age III, so there can be only two marine annuli, which are labeled as II and III in figure 8. The narrow band (i) between these two annuli must therefore be regarded as an incidental check.

From the standpoint of age determination, it is imperative that an ocean nucleus and a stream nucleus can be positively identified, for it will make a difference of 1 year in age, depending upon whether an annulus or a check is assigned to the central fine circuli area. No definite criteria can be found in literature that positively differentiate a mere check from a genuine annulus in this nuclear area of growth in chinook scales. Determination of age is usually based on the appearance of the nuclear zone and is highly dependent upon personal judgment. Thus, a stream nucleus has been described as an area of many closely placed circuli bounded by a distinct narrow band of more closely spaced circuli, the annulus. An ocean nucleus, on the other hand, is recognized when the nuclear zone consists of relatively few but wider circuli that are not marked off by a distinct check from the ensuing widely spaced marine growth.

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[8] The term "sub-one" is derived from the subscript of Gilbert-Rich's (1927) scale formula, for example, 3_1, 4_1.

Unfortunately, nuclear zones of many chinook salmon scales are not clearly defined so that the morphology of the nuclear zones alone does not enable us always to differentiate with certainty the ocean nuclei from the stream nuclei. If, for example, the scales in figures 7 and 8 had come from fish of unknown age, we would have no real basis for calling one mark a mere check (C) and the other a true annulus (I).

Obviously, something other than visual determination must be devised. As we had available a large number of scale samples from recaptured marked chinook salmon comprising both the stream type and the ocean type of nuclear growth, we were able to compare the characters of these two groups of scales on a quantitative basis. Because the nuclear zones of circuli failed to show significant differences, our study was extended to cover marine growth as well, and we have developed some criteria that help to guide the chinook scale reader to differentiate ocean from stream nuclei on a more objective basis.

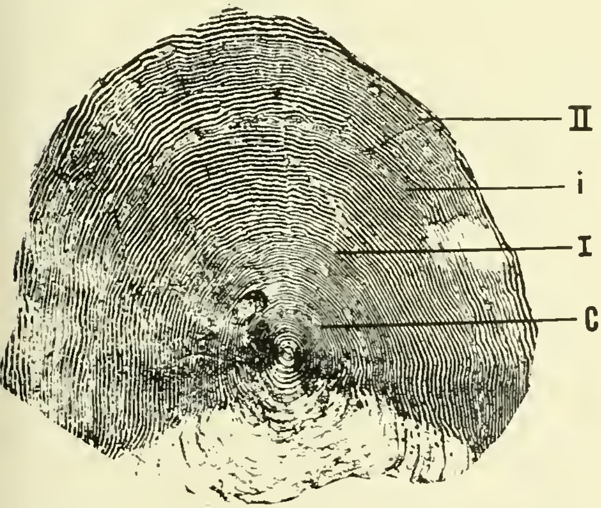

FIGURE 9.—A scale of adult chinook salmon that was released as a fingerling in July at the Little White Salmon Hatchery (July 1957 release, 1959 return.

Before we discuss quantitative measurements, let us examine some scales of adult chinook that originated from releases during the intermediate period between May of the first year and February of the next year, to observe the transition from ocean nucleus growth type to stream nucleus growth type.

A scale of a July release origin is shown in figure 9. Being similar to the scale of a May release origin (fig. 7), it also shows an ocean nucleus (I) and a strong check (C) for the nuclear area. Based on the known age of this

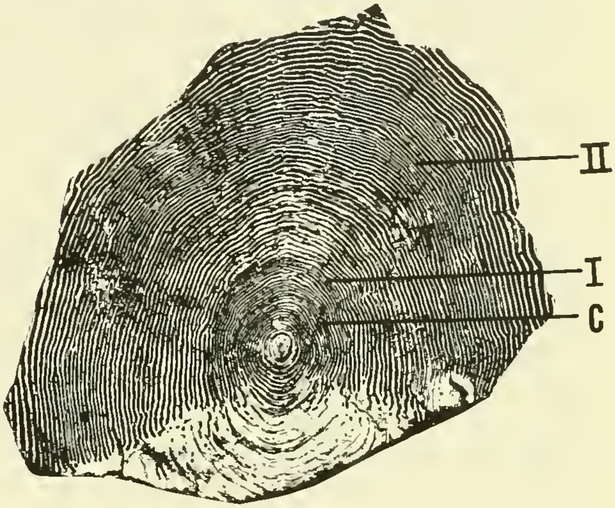

FIGURE 10.—A scale of adult chinook salmon that was released as a fingerling in September at the Little White Salmon Hatchery (September 1958 release, 1960 return).

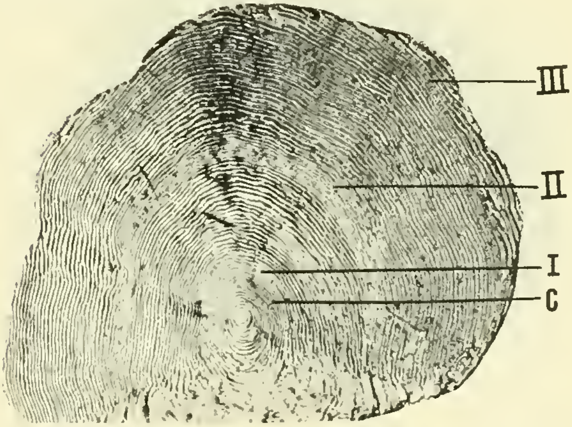

FIGURE 11.—A scale of adult chinook salmon that was released as a fingerling in September at the Little White Salmon Hatchery (September 1957 release, 1960 return).

fish, we know that "I" marks an annulus and "C" is merely a check. An incidental check (i) is also present between annuli I and II.

Two scales of adults that came from September release are shown in figures 10 and 11. In figure 10, the marine growth of the first year (C to I) is much reduced as compared with the scale of May or July release origin (figs. 7 and 9). Consequently, the annulus (I) is getting closer to the check (C), and the entire ocean nucleus becomes much smaller in size. Because of this, it is easy to determine that the check (C) here is not an annulus. Further reduction in the first year's marine growth is seen in the second example of a September release (fig. 11). Here the entire nuclear zone assumes the appearance of a stream nucleus. Indeed, it is questionable whether there is any amount of true marine growth inside the first annulus (I).

A scale of the October release origin (fig. 12) shows the same characteristics, i.e., a much reduced zone between "C" and "I," and a nuclear zone that assumes the look of a stream nucleus. At least, as far as age determination is concerned, because the total age of this fish is known to be III, it is certain that "I" is the first and only annulus up to that point, much as "I" in a typical stream nucleus such as that of a February release origin (fig. 8).

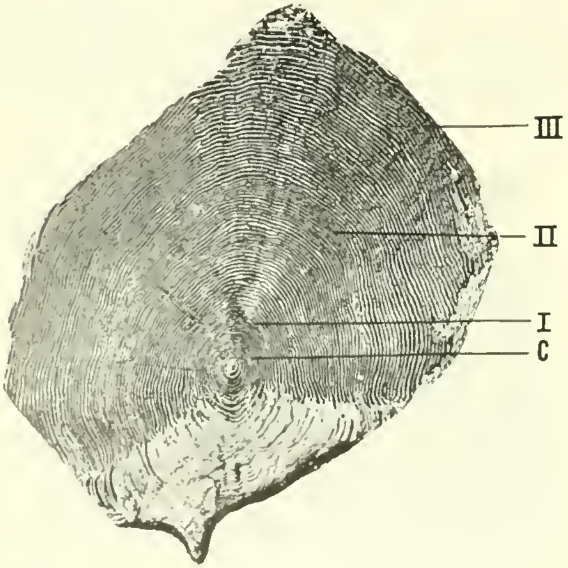

FIGURE 12.—A scale of adult chinook salmon that was released as a fingerling in October at the Little White Salmon Hatchery (October 1957 release, 1960 return).

From the above series of examples, it is evident that when the young chinook salmon were released as hatch-of-the-year from May through July, they entered the ocean during the growing season of the first year after some sojourn in the river. As a result, there was a large number of wide marine circuli outside the central zone of narrow fresh-water circuli, resulting in a large ocean nucleus. As the release date became later and later in the year (September and October), however, the chinook salmon would miss more and more of the current season's marine growth, and the result was a nuclear type similar in appearance to a stream nucleus. Finally, when the young chinook salmon were reared in fresh water over winter and were not released until February of the second year, the nuclear zone was composed solely of fresh-water growth, and any marine growth belonged to the following year. For all practical purposes, scales from September and October releases should be treated as stream nucleus type, for there is no way of knowing that "I" is not a stream annulus without the knowledge of release date.

Because the fresh-water growth part in an ocean nucleus may not be distinguishable from that of a stream nucleus, we extended our study into the marine growth of the first and second years of ocean life to find differences between these two types. In this study, 72 returns from May and July releases were treated as one group representing the ocean nucleus type, and 85 returns from October and February releases were treated as another group representing the stream nucleus type.

The method consists of first locating the apparent first marine annulus, i.e., a band of narrow circuli after a zone of wide circuli. This is "I" in figures 7 and 9 and "II" in figures 8, 11, and 12. Then, from the midpoint of this annulus band 20 circuli were counted outward toward the edge of the scale along an antero-lateral radius, and the total distance of these 20 circuli was measured and represented by "A." This represents the major part of the second year growth in ocean for both groups of scales. Similarly, 20 circuli were counted inward toward the focus and the total distance was measured as "B" (fig. 13), which represents the first year growth in ocean for both groups of scales. Then we computed the ratio of A/B, which is the ratio of second year marine growth to the first year marine growth.

We found that in the May to July release group, circuli of the second year marine growth (A) were, on the average, nearly 50 percent wider than the first year marine growth (B); whereas in the October to February release group, "A" was only 22 percent wider than "B". The frequency distribution of the ratio A/B of these two groups of scales is shown in figure 14. It is obvious that the two groups are distinctly different in the value of A/B, but there is also enough overlap so that not all scales can be identified to their nuclear growth type on this character alone.

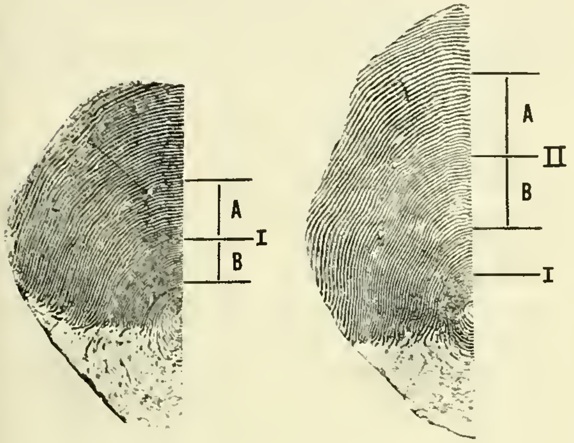

FIGURE 13.—The measurement of circulus spacing. Left, chinook scale with an ocean nucleus; right, chinook scale with a stream nucleus.

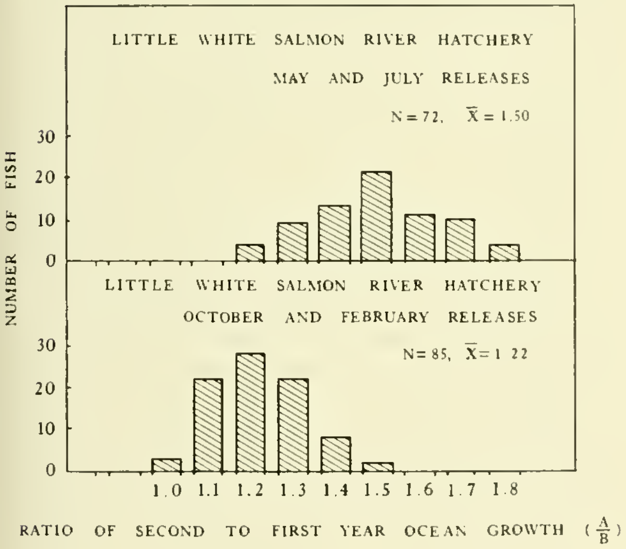

FIGURE 14

FIGURE 14.—Frequency distribution of the ratio of second to first year marine growth (A/B) of little white salmon Hatchery recaptures of May and July releases, and October and February releases.

DIFFERENTIATION OF FALL CHINOOK AND SPRING CHINOOK SCALES BY MARINE GROWTH

The fall chinook scales normally have a typical ocean nucleus (sub-one age), and the spring chinook scales normally have a typical stream nucleus (sub-two age). The nuclear growth part of these two types of scales cannot always be distinguished. So in order to identify these two groups of fish, we applied the method of comparing first and second year's marine

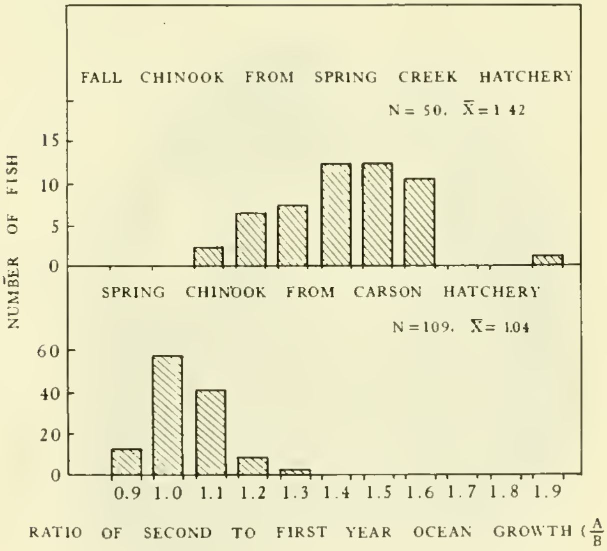

FIGURE 15

FIGURE 15.—Frequency distribution of the ratio of second to first year's marine growth (—A/B) of fall chinook and spring chinook.

growth as developed from the study of Little White Salmon Hatchery mark recovery specimens. For study material, we used scales collected from unmarked fall chinook at Spring Creek Hatchery and those collected from unmarked spring chinook at Carson Hatchery.

Scales of 50 fall chinook and 109 spring chinook were measured. The frequency distributions of the ratio of second year's to first year's marine growth A/B of these two groups of fish are shown in figure 15. These distributions show clearly that fall and spring chinooks are distinctly separate groups as far as the character of marine growth is concerned. The difference between the two groups is similar to that between May to July release group and October to February release group of Little White Salmon Hatchery fall chinook. In other words, the fall chinook are similar to May to July release group in having a large A/B ratio, and the spring chinook are similar to October to February release group of fall chinook in having a small A/B ratio.

The outstanding feature of spring chinook scales is that the marine growth of the first year is nearly as good as that of the second year, so that its A/B ratio approximates 1.0, as compared with 1.2 for the fall chinook released in October to February. In fact, this character alone is often sufficient to distinguish a spring run from a fall run of chinook salmon. An example of a spring chinook scale is shown in figure 16, in which the circuli inside of the first marine annulus (II) are as widely spaced as circuli outside of it.

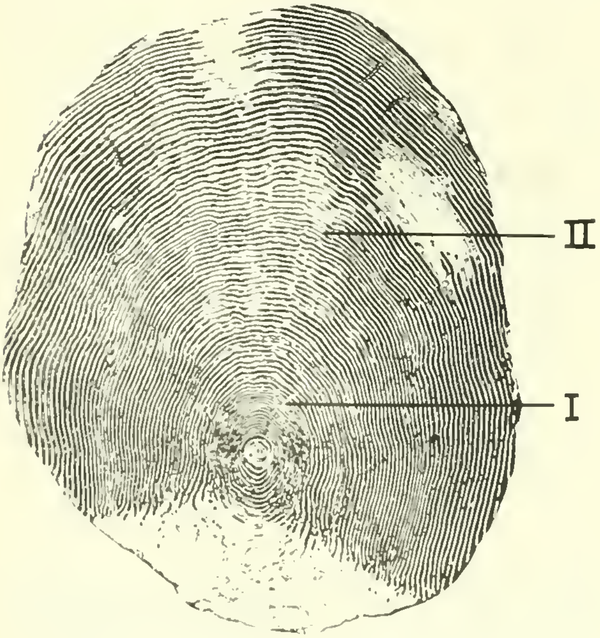

FIGURE 16.—A scale of a spring chinook salmon.

SUMMARY AND CONCLUSIONS

Scales of Columbia River chinook salmon were studied to find answers to the following questions:

1. Is it possible, from structures of adult chinook scales, to identify whether a fish has originated from fry or fingerling migrant?

The answer is negative. Scales from marked fish recoveries showed that there was no significant difference in the mean values of circulus spacing in nuclear growth part between chinook salmon released as fry and those released as fingerlings, although the spacing is more variable in the fry than in the fingerling group. In the first marine growth, circuli in the group released as fry are more widely spaced than in the group released as fingerlings. While the difference is statistically significant, there was too much overlap so that identification of individual scales was not possible.

2. Can the effect of marking, if any, on growth of chinook salmon be detected by scale studies?

The answer is positive. At the Spring Creek Hatchery, fall chinook fingerlings were marked by removal of adipose and right pectoral fins. When scales from marked fish recoveries were compared with those from unmarked fish returns, circulus spacing in marine growth of the marked group was found narrower than the unmarked group.

3. How do the scales of early season (May-July) releases of fall chinook differ from those of later season (October-February) releases?

In answering the above question, we found some interesting relations between scale growth patterns and times of release. Early season releases of fall chinook resulted in an ocean nucleus type (sub-one age) that is typical of fall chinook scales. Late season releases, however, resulted in a stream nucleus type (sub-two age) resembling that of spring chinook scales. Moreover, these two groups of scales are different in marine growth patterns. When circulus spacing in the second year marine growth is compared with that in the first year marine growth, the ratio is far greater for the sub-one group than for the sub-two group.

4. Can fall chinook scales be separated from spring chinook scales by objective means?

The answer is positive. Fall and spring chinooks can be differentiated by their scales. Differentiation, however, is not made from nuclear growth patterns as is usually done visually, but is achieved objectively by comparing marine growth circuli of the first 2 years, the same technique as used for early-season and late-season releases of fall chinook. In the spring chinook, circuli in the second year of marine growth are nearly 50 percent more widely spaced than those in the first year; whereas in the fall chinook, they are about the same.

ACKNOWLEDGMENTS

The most important ground work in connection with the present paper had been done before we started our studies, for marking experiments on the Columbia River chinook salmon and collecting scale samples and pertinent data had been performed by the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. Paul Zimmer, Harlan E. Johnson, and Roy Wahle of the Bureau provided the study material and data. The Fish Commission of Oregon and the Washington State Department of Fisheries, which are also studying the Columbia River chinook salmon, supplied additional material and information, and in this connection, I was assisted by Sigurd J. Westrheim, Raymond A. Willis, and Robert N. Thompson of the former organization and Peter Bergman of the latter agency. Charles E. Walker of the Canadian Department of Fisheries in Vancouver, British Columbia, sent us some duplicate scale impressions of Big Qualicum chinook salmon for our study, and Gerald J. Paulik of the Fisheries Research Institute of the University of Washington advised us on the statistical treatment of the data.

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CATCH AND ESTIMATES OF FISHING EFFORT AND APPARENT ABUNDANCE IN THE FISHERY FOR SKIPJACK TUNA (*KATSUWONUS PELAMIS*) IN HAWAIIAN WATERS, 1952–62

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ABSTRACT

Detailed data on catch and effort are obtained each year from all vessels that fish full time in the Hawaiian skipjack tuna fleet. These data permit description of the fishery and inferences about the abundance of skipjack. Our past measures of abundance have been stated in terms of total catch and catch per unit of effort calculated in terms of productive trips of all sizes of vessel. This study offers information on changes in the apparent abundance of skipjack in Hawaiian waters calculated from standardized units that will be unaffected by changes in the numbers of small and large vessels in the fishing fleet.

Effort was measured in terms of an "effective" trip, which was defined as a trip in which skipjack were caught. Bias introduced by the lack of data on zero-catch trips is discussed.

The number of men hooking per trip declined in 1950–60; however, those that remained in the fishery increased their catch rate by shifting their emphasis in fishing technique from "grasping and unhooking" each fish to "flipping," a method in which the fisherman swings the fish aboard and by relaxing the tension on the pole, permits the hook to fall clear of the fish's mouth. The higher catch rate from the "flipping" method was one of the factors that offset the effect of the decline in the number of men. Another factor that appeared to increase the catch rate was the reduction in the number of small vessels that did poorly.

The vessels were separated into two size classes: Class 1, with bait-carrying capacities of less than 800 gallons per baitwell; Class 2, with bait capacities of more than 800 gallons per baitwell.

The catch was standardized to Class 2 vessels. The catch per standard effective trip (Y/f) and the total catch fluctuated similarly in all years. The Y/f had no apparent trend and averaged about 5,700 pounds. The Y/f and the relative effective fishing intensity were not correlated significantly over the 11-year period. Year-to-year changes in apparent abundance seem to be independent of changes in fishing effort.

I concluded that variations in the availability and vulnerability of skipjack contribute to fluctuations in landings. The variations in strength of year classes also may have contributed importantly to fluctuations in the landings.

In Hawaii, the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), or aku, as it is called locally, supports the State's most important commercial fishery, contributing about 66 percent by weight to the total Hawaiian marine catch, and accounting for about 40 percent of the total annual ex-vessel value. The fish are caught exclusively by pole and line from schools which are concentrated at the stern of the vessel by chumming with live bait. The fishery is highly seasonal. Landings have ranged from about 29,000 pounds in January, typically a poor month, to about 3.7 million pounds in July, when the catch usually is large. Four- to 5-pound fish usually are caught throughout the year, but between May and September, larger fish, ranging between 13 and 25 pounds, are also taken. The latter contribute a large percentage by weight to the total annual catch. Not only does the catch fluctuate by month but also by year. In 1952–62, the yearly landings ranged between 6.1 and 14.0 million pounds, apparently with changes in the numbers of the larger fish at the islands.

In the past, abundance of skipjack tuna in Hawaiian waters has been measured in terms of total catch and catch per unit of effort calculated in productive trips of all sizes of vessels —uncorrected fishing effort (Yamashita, 1958; Shippen, 1961). In general, total catch is not a dependable measure of abundance, because it is affected seriously by changes in the amount

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of fishing effort and by weather and sea conditions. Catch per unit of effort calculated in terms of uncorrected fishing effort is also unreliable because it varies from year to year with changes in the fishing fleet. The fleet is made up of vessels of different sizes, and numbers of these change as some enter and some leave the fishery. Both size and number affect the catch per unit of effort. An important phase of this study is the derivation of a measure of abundance of skipjack in Hawaiian waters based on catch per unit of effort in standardized units that are unaffected by changes in the fishing fleet.

SOURCES OF MATERIALS

The basic data for this study were obtained from Fish Catch Reports (January 1952 to June 1954) and Aku Catch Reports (July 1954 to December 1962) submitted by the fishermen to the Hawaii Division of Fish and Game. Catch reports of only those vessels that fished for skipjack tuna full time were used. The report form has undergone several revisions through the years, but all versions have carried spaces for the following information: The date of landing, the pounds of skipjack caught, and the fishing area. Yamashita (1958) described the method of reporting the areas fished by a skipjack vessel. Briefly, a fisherman reports only the code number corresponding to the statistical area where the catch was made. These areas are indicated on the Division of Fish and Game's Fisheries Chart No. 2 (see Yamashita, 1958: fig. 2).

Data on number of men hooking per trip were obtained from Aku Boat Interview Sheets (January 1950 to July 1956), which were collected and checked by the personnel of the Division of Fish and Game, from logbook records (1957–59), and from Sampan Interview Records (August 1959 to June 1961).

DESCRIPTION OF THE FISHERY

The present brief description of the fishery and review of fishing operations is based on June (1951). The number of skipjack tuna sampans fishing full time reached a maximum of 28 in 1951, but since then has declined; in 1963 only 20 vessels were fishing full time for skipjack. The vessels, generally of wooden construction, range from 58.3 to 80.5 feet in registered length and from 27 to 77 in gross tonnage. These vessels carry 6 to 14 men per fishing trip.

The nehu or anchovy, *Stolephorus purpureus* Fowler, makes up about 92 percent of the bait catch; a second bait is the iao or silverside, *Pranesus insularum* (Jordan and Evermann). Each vessel catches its own bait, fishing day and night until a sufficient supply is obtained. All the vessels have six baitwells with screened holes at the bottom through which sea water circulates.

The Hawaiian skipjack tuna fishermen usually confine their fishing and scouting operations to waters within 90 miles of the main islands. Skipjack on the fishing ground are indicated to the fishermen almost exclusively by bird flocks which are often associated with schools of fish. When a school has been sighted the captain attempts to intercept it. Once the head of the school is reached, water sprays are turned on and the "chummer" scatters live bait into the water. If the skipjack bite, the fishermen begin fishing off the stern. Fishing continues until the bait supply is exhausted or until the captain decides that further fishing is not worthwhile. If chumming is unsuccessful, the school is abandoned and scouting is resumed. The sampans may encounter several skipjack tuna schools during the day, but the fish may bite in only about half of them. Scouting and fishing are discontinued as dark approaches, and the vessels usually head for port to unload the day's catch.

TRENDS IN CATCHES OF SKIPJACK TUNA

To show the trends in catches of skipjack tuna from Hawaiian waters, catch statistics were summarized by months and quarters for each year and by two broad geographical areas. Comments on the trends of catches are based on tabulation of data for 1952–62; therefore, the results may not be in complete agreement with those published for 1948–53 by Yamashita (1958).

Table 1.—*Monthly, quarterly, and annual catches of skipjack tuna in Hawaii, 1952-62*

[Thousands of pounds]

Period of time	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	Range	Average
Month:													
January	29	200	271	98	322	524	638	215	242	492	459	29-638	317
February	90	204	185	118	281	133	236	107	179	247	412	90-412	199
March	56	576	359	263	230	454	151	397	327	600	199	56-600	328
April	387	864	759	681	433	331	792	839	411	620	480	331-864	600
May	578	1,240	1,132	1,399	1,375	816	277	1,757	842	930	1,178	277-1,757	1,048
June	818	2,241	2,804	2,197	1,926	812	948	1,679	776	2,721	2,308	776-2,804	1,748
July	1,654	1,510	3,705	1,824	2,321	919	1,405	2,382	1,430	2,288	1,809	919-3,705	1,932
August	1,758	2,142	2,178	1,170	1,586	698	1,191	1,815	1,396	1,359	922	698-2,178	1,474
September	987	1,281	1,049	993	1,055	489	631	1,377	690	705	568	489-1,377	893
October	576	1,199	1,121	440	725	530	186	1,064	439	516	525	186-1,199	666
November	110	218	390	272	635	282	144	626	219	213	170	110-635	298
December	249	384	68	239	243	142	235	155	409	203	385	68-409	246
Quarter:													
First	175	980	815	479	833	1,111	1,025	719	748	1,339	1,070	175-1,339	845
Second	1,783	4,345	4,695	4,277	3,734	1,959	2,017	4,275	2,029	4,271	3,966	1,783-4,695	3,395
Third	4,399	4,933	6,932	3,987	4,962	2,106	3,227	5,574	3,516	4,352	3,299	2,106-6,932	4,299
Fourth	935	1,801	1,579	951	1,603	954	565	1,845	1,067	932	1,080	565-1,844	1,210
Annual	7,292	12,059	14,021	9,694	11,132	6,130	6,834	12,413	7,360	10,894	9,415	6,130-14,021	9,749

MONTHLY, QUARTERLY, AND ANNUAL CATCHES

The seasonal character of the Hawaiian skipjack tuna fishery is shown by the monthly and quarterly catches in 1952–62 (table 1). The catch usually increased gradually from April to a peak in June, July, or August and then declined progressively to a low level in December. Usually February had the smallest catch and July the largest. Also, the catch usually rose in January following the progressive decline from the summer peak to December.

The quarterly catches showed the same trend as the monthly landings. First-quarter catches were usually the smallest and averaged 0.8 million pounds. Second-quarter catches reflected the increased fishing activity during the spring and averaged about 3.4 million pounds. Third-quarter landings were rather consistently the largest and averaged 4.3 million pounds; only in 1955 and 1962 did second-quarter catches exceed those of the third quarter. The fourth-quarter catches declined to an average of 1.2 million pounds.

The variations of the annual catches were large. In 1952–62, there were 4 poor years—1952, 1957, 1958, and 1960—in which the catches were far below the 11-year average of 9.7 million pounds. The catches in 1955 and 1962 were close to the 11-year average, and those of the remaining years were above average. The maximum catch of 14.0 million pounds occurred in 1954; the minimum of 6.1 million pounds was in 1957.

INSHORE AND OFFSHORE CATCHES

For this study, I consider the inshore area to extend from the coastline to 20 miles at sea and the offshore area to include all statistical areas beyond 20 miles from the coastline.

The catch reports used in this study were from vessels that fished for skipjack full time. The total weight landed by these vessels and the effort expended to produce it are hereafter called sample catch and sample effort. In addition to the catches made by these vessels, catches were made by vessels that fished for skipjack tuna only part time. The total weight landed by vessels that fished full time and those that fished part time is hereafter called total catch and the effort expended to produce it is total effort. Data on total catch were obtained from annual summaries of catch issued by the Hawaii Division of Fish and Game.

I obtained the sample catch (all areas) and the sample inshore catch from the catch reports, and from these data, I calculated the percentage of the catch made inshore. The total inshore catch was estimated by applying the percentage of the catch made inshore to the total catch. The estimated annual inshore catches (table 2) are shown in relation to the total catch and the estimated total offshore catch in figure 1.

The percentage of the catch made inshore ranged from 63 percent in 1954 to 90 percent in 1960. During the poor years—1952, 1957, 1958, and 1960—the inshore catch averaged 83 percent of the total catch, whereas in

Table 2.—*Estimated total inshore and total offshore catches of skipjack tuna in Hawaiian waters, 1952–62*

Year	Sample catch all areas	Percentage of sample catch inshore	Actual total catch	Estimated inshore catch	Estimated offshore catch
	Thousand pounds	*Percent*	*Thousand pounds*	*Thousand pounds*	*Thousand pounds*
1952	6,277	76	7,292	5,542	1,750
1953	10,543	66	12,059	7,959	4,100
1954	11,229	63	14,021	8,833	5,188
1955	8,257	83	9,694	8,046	1,648
1956	10,937	73	11,132	8,126	3,006
1957	6,075	80	6,130	4,904	1,226
1958	6,494	86	6,834	5,877	957
1959	11,945	83	12,413	10,303	2,110
1960	7,107	90	7,360	6,624	736
1961	10,780	78	10,894	8,497	2,397
1962	9,086	82	9,415	7,720	1,695

average and good years the inshore catch averaged 75 percent.

Yamashita (1958) who examined the 1948–53 catches of skipjack tuna suggested that about 8.0 million pounds may be nearly the maximum that can be obtained in the inshore area. The present study indicates, however, that the inshore catch can be well above this level. The 1959 landings, for example, were 10.3 million pounds and were caught by a fleet of 21 full-time vessels, although in 1949–53 26 to 28 vessels were fishing full time for skipjack.

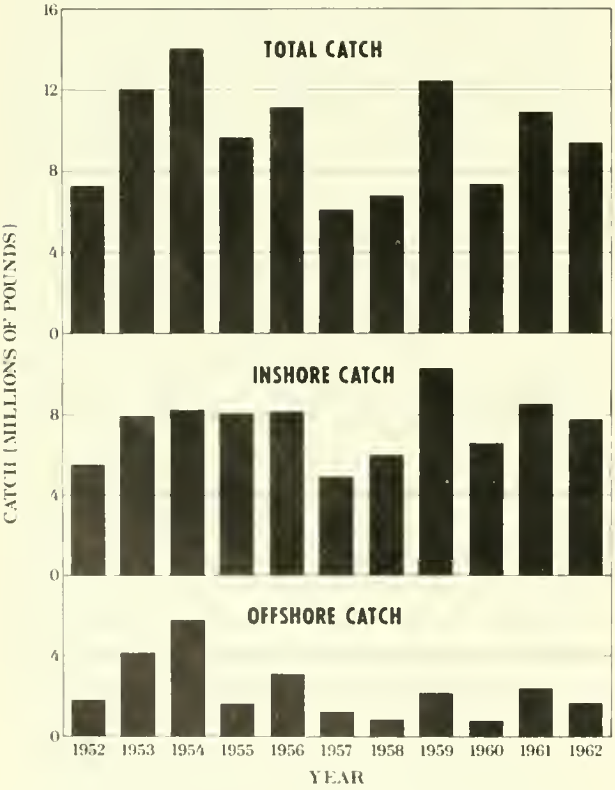

Figure 1.—Total catch of skipjack tuna (all areas) and the estimated inshore and offshore catches in the Hawaiian fishery, 1952-62.

The offshore catch increased gradually from 1.8 million pounds in 1952 to a peak of about 5.2 million pounds in 1954 (fig. 1). After a sharp decline to about 1.6 million pounds in the following year, the offshore take fluctuated between 0.8 and 3.0 million pounds from 1956 to 1962.

FISHING INTENSITY

Fishing intensity is the total amount of effort expended in catching fish. Effort changes with time in different ways. For example, in a fishery where a trip is considered a unit of fishing effort, an increase in the duration of trips or an increase in the fishing power of vessels alters the unit of effort. These changes complicate the analysis of catch and effort data; therefore it becomes necessary to obtain and examine information on size of vessels, on modification of or improvement to fishing gear, and on changes in fishing time.

SIZE CLASSES OF VESSELS

It may be expected that size of a vessel influences its potential efficiency as a fishing unit in a pole-and-line fishery because the larger crews give the larger vessels greater fishing power. One measure of effort is the number of men aboard per trip; this number may vary among vessels and with the years. The interview records for 1950–56 indicated that the number of men aboard per trip varied between 6 and 14.

The effects of this crew variability were reduced by separating the vessels arbitrarily into two size classes according to their bait-carrying capacities. The bait-carrying capacity was a good measure of the vessel's fish capacity, because on the return to port the empty baitwells were used to store the catch. The vessels with large bait capacities were the large ones that usually carried more men. Data on the bait capacity of most of the vessels in the fleet were given by Yamashita (1958; appendix table 1).

The bait capacity of a vessel is stated in terms of the average effective volume in gallons per baitwell and is derived from the length of the baitwell, its width, and its depth up to the water level.

The size classes of vessels used in this study are as follows:

Class 1.—Bait capacity up to 800 gallons per baitwell; registered length, 58.3 to 71.9 feet; gross tonnage, 27 to 54 tons; engine, 110 to 450 horsepower. Their number ranged from 8 to 16 in 1952–62.

Class 2.—Bait capacity more than 800 gallons per baitwell; registered length, 65.0 to 80.5 feet; gross tonnage, 45 to 77 tons; engine, 160 to 600 horsepower. Their number ranged from 11 to 14 in 1952–62.

It was necessary to estimate the bait-carrying capacity of four vessels for which Yamashita (1958) gave no records. To determine the most dependable procedure, characteristics such as gross tonnage, net tonnage, registered length, and engine horsepower, were examined in relation to average effective volume of baitwells. The regression of average effective volume per baitwell (Y) on gross tonnage (X) (fig. 2) proved to have the smallest error of estimate. This relation was used therefore, to estimate the average effective volume of the four vessels.

THE EFFECTIVE TRIP AS A MEASURE OF EFFORT

The records used carried three types of statistics from which one might estimate effort: The number of men hooking per trip, the number of men aboard per trip, and the number of trips. The number of men hooking per trip and the number of men aboard per trip were not consistently entered; therefore, I selected the number of fishing trips as the unit of effort. The catch reports showed all trips on which a catch was made, but gave no indication of zero-catch trips. For this study I define effort as an effective trip (a trip on which skipjack tuna were caught).

Because zero-catch trips were not recorded, effort always is underestimated. The extent of the underestimate may not be serious in some years, because zero-catch trips are fewer when fishing is good (Shippen, 1961). This source of error can weigh heavily, however, in a year of poor fishing, when zero-catch trips become numerous.

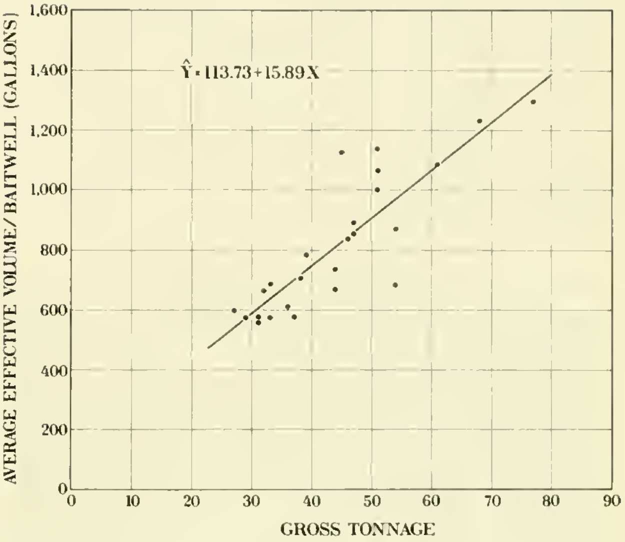

FIGURE 2.–Regression of average effective volume per baitwell on gross tonnage of Hawaiian skipjack tuna vessels.

ESTIMATES OF ZERO-CATCH TRIPS

Because only the number of effective trips is known from the catch reports, estimates of catch per effective trip (Y/g) are larger than if total effort had been used, assuming that zero-catch trips occur from time to time. (The notation Y refers to the total weight of fish in the catch and g to the fishing effort or effective trip as recorded. In a later section of this paper the notation f is used to refer to fishing effort expressed in standard effective trips.) A measure of effort, however, should reflect zero-catch trips as well as those on which fish were caught.

Logbook records available for a few vessels in 1957–59 provided some data on zero-catch trips (table 3). Five vessels kept logbooks in 1957, seven in 1958 and five in 1959; the vessels represented 20, 29, and 24 percent of the fleet.

TABLE 3.—*The total catch, number of Class 1 and Class 2 vessels sampled, their total recorded trips, and number and percentage of zero-catch trips, Hawaii, 1957–59*

Year	Total catch	Class 1				Class 2			
		Vessels	Trips	Zero-catch trips		Vessels	Trips	Zero-catch trips	
	Thousand pounds	*Number*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Number*	*Percent*
1957	6,130	2	181	51	28	3	357	136	38
1958	6,834	2	145	31	21	5	482	131	27
1959	12,413	1	93	2	2	4	336	32	10

Because no additional data are available, I assumed that this sample represents the fleet's activities for these years.

Zero-catch trips were more frequent among Class 2 than among Class 1 vessels (table 3). The higher rate of occurrence in poor years (1957–58) than in the good year (1959) indicates that the percentage of zero-catch trips tends to decrease as total catch increases. The apparent negative correlation between these variables is supported to some extent by Shippen (1961: table 2) who analyzed the logbooks of two vessels. (The original records show that these were Class 2 vessels.) He found that in a poor year (1952), zero-catch trips accounted for 10 percent of the total trips made by Boat A and 14 percent of those made by Boat B. In a good year (1953), zero-catch trips were 8 and 10 percent for Boat A and Boat B, respectively.

The numbers of effective trips and zero-catch trips were used to estimate the total effort for 1957–59. For example, in 1957, the total number of zero-catch trips among Class 1 vessels was estimated by simple proportion to be 262. The estimated total effort for both size classes for 1957–59 is given in table 4.

TABLE 4.—*Number of effective trips and estimated number of zero-catch trips of Class 1 and Class 2 vessels, Hawaii, 1957–59*

Year	Vessels	Class 1			Class 2		
		Effective trips	Estimated zero-catch trips	Estimated total trips	Effective trips	Estimated zero-catch trips	Estimated total trips
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
1957	25	668	262	930	910	560	1,470
1958	24	659	179	838	865	323	1,188
1959	21	779	17	796	1,055	111	1,166

The number of zero-catch trips was large in 1957 and 1958. In 1957 the estimated total number of unreported zero-catch trips was 822, or an average of about 33 per vessel; in 1958 the estimated number was 502 or about 21 per vessel. In 1959, a good year in the fishery, the estimated number of zero-catch trips for the fleet was only 128—about 6 per vessel.

The results indicate that catch per effective trip should be regarded with caution. Effective effort is a biased measure of fishing pressure, but it has been used because information on zero-catch trips was not available from the catch reports used. This condition has been remedied; in July 1964, the Hawaii Division of Fish and Game issued revised catch-report forms which have spaces for recording zero-catch trips.

DURATION OF AN EFFECTIVE TRIP

Most of the vessels in the fleet made short runs. They left for the fishing grounds in the early morning and returned to port in the evening. On occasion, however, trips of 2, 3, or 4 days have been recorded. Only a small proportion of the day was devoted to actual fishing; the greater part was spent scouting for bird flocks that follow schools of skipjack tuna.

To judge the possible effects of longer trips, the frequency of occurrence of 1- and multiple-day trips (2 or more days per trip) was determined from 1960 interview records for 16 vessels (table 5). Records for a total of 329 trips showed 315 of 1 day (95.7 percent), 13 of 2 days (4.0 percent), and 1 of 3 days (0.3 percent). Of the thirteen 2-day trips, 9 had catches during both days at sea, but each of the

TABLE 5.—*Number and percentage of 1-, 2-, and 3-day trips, total catch, catch per effective trip, and range of catches of 16 Hawaiian skipjack tuna vessels in 1960*

Days per trip	Effective trips		Catch		
			Total	Per effective trip	Range
Number	*Number*	*Percent*	*Pounds*	*Pounds*	*Pounds*
1	315	95.7	1,636,185	5,194	375-39,553
2	13	4.0	121,462	9,343	2,000-17,000
3	1	.3	35,000	35,000	....
Totals	329	....	1,792,647	....	....

remaining 4 had only 1 day in which skipjack tuna were caught. We may conclude that a trip usually represents 1 day's fishing.

AVERAGE NUMBER OF MEN HOOKING PER EFFECTIVE TRIP

The number of hooks fishing on a Hawaiian skipjack tuna vessel depends on the number of fishermen that take fishing positions along the stern during the fishing operation, since each man fishes a single pole to which a line and feathered jig is attached. Yuen (1959), in a study of the response of skipjack tuna to live bait, pointed out that the number of men hooking was one of the factors that affect the catch per school. The catch per effective trip is also related to the number of men hooking; it is important, therefore, to examine the year-to-year variation in this number. Data on the number of men hooking were available only from records collected between 1950 and 1960; those for 1950–56 and 1960 were from interview records and those for 1957–59 were from logbooks. These data were used to calculate monthly and annual averages by size classes of vessels (table 6).

TABLE 6.—*The monthly and annual average of the number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60*

Month and class		1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
Jan.	1	-----	-----	-----	-----	-----	-----	6.0	6.0	7.1	-----	7.0
	2	-----	-----	-----	-----	-----	11.0	8.3	7.2	7.2	-----	7.9
Feb.	1	-----	-----	-----	-----	-----	8.0	6.0	5.7	6.7	-----	8.2
	2	-----	-----	-----	-----	-----	-----	8.3	6.3	6.8	-----	7.9
Mar.	1	-----	-----	-----	8.8	9.9	9.3	-----	6.8	6.9	-----	7.1
	2	-----	-----	-----	9.6	10.0	10.3	10.0	6.6	7.3	-----	7.4
Apr.	1	-----	-----	-----	9.5	9.3	9.2	7.3	6.5	7.1	7.4	6.7
	2	-----	-----	-----	9.3	9.7	9.6	10.0	7.2	7.7	7.1	7.0
May	1	8.4	8.2	9.3	9.3	9.4	9.2	7.2	6.7	6.0	6.8	6.6
	2	10.6	10.0	9.0	9.4	10.5	9.7	-----	8.1	8.2	8.0	7.0
June	1	8.8	8.0	8.0	8.8	9.2	9.3	7.1	6.7	7.1	8.6	7.4
	2	10.2	10.7	9.7	9.4	9.7	-----	-----	8.2	8.7	7.8	7.3
July	1	8.8	7.9	8.2	8.0	8.5	8.8	7.7	7.0	8.9	8.9	6.8
	2	9.7	8.5	9.7	9.8	9.5	9.2	-----	8.2	8.7	7.3	7.7
Aug.	1	8.6	8.7	8.5	8.6	8.4	8.2	-----	6.3	7.9	8.4	6.5
	2	10.8	9.7	9.1	10.3	10.1	8.3	-----	7.4	8.5	7.2	7.6
Sept.	1	7.4	8.8	9.1	6.5	9.5	7.5	-----	5.5	5.7	7.5	6.5
	2	10.7	9.1	9.1	10.2	9.4	7.4	-----	7.8	7.8	6.9	6.8
Oct.	1	-----	6.2	7.8	7.9	8.5	8.0	-----	7.2	6.1	6.9	7.3
	2	-----	8.7	8.6	-----	9.4	7.0	-----	6.7	8.0	6.6	6.7
Nov.	1	-----	-----	8.7	9.9	10.0	8.0	-----	7.3	6.4	6.2	5.0
	2	-----	7.0	7.0	9.9	11.9	6.0	-----	6.5	8.3	6.9	5.0
Dec.	1	-----	-----	-----	-----	-----	-----	-----	8.0	6.6	7.0	6.5
	2	-----	-----	-----	9.3	11.0	6.1	-----	6.8	7.9	6.7	6.4
Annual average	1	8.4	8.2	8.4	8.6	9.2	8.9	7.1	6.7	7.1	7.6	6.9
	2	10.4	9.6	9.2	9.7	9.8	8.3	8.7	7.4	8.1	7.2	7.4

I expected that the number of men hooking per effective trip would be greater during the season months (May to September) than during the off-season months (Shippen, 1961). Despite the incompleteness of the data for some years, the trend of change, discernible from the data for those years where information was adequate, indicates no pronounced increase in the number of men hooking in May to September (fig. 3). More men fished per effective trip in Class 2 than in Class 1 vessels, although the 1959–60 data indicate that the differences between the two classes were small.

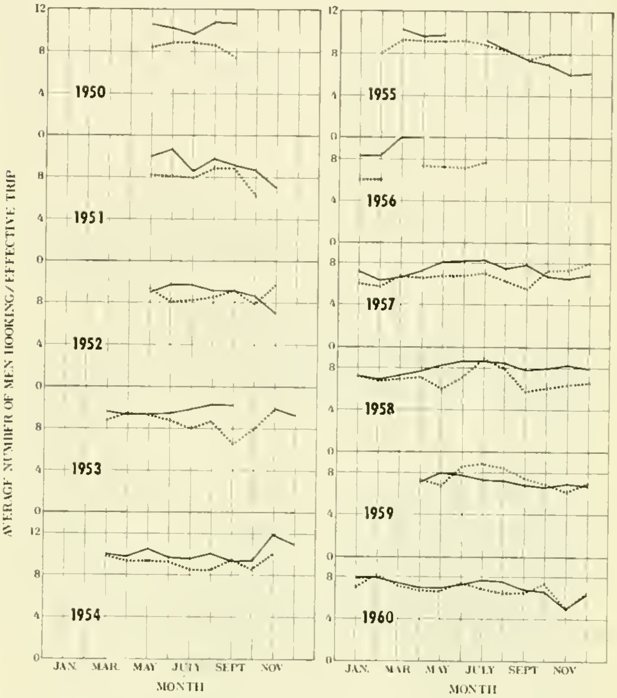

FIGURE 3.—Monthly averages of number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60. Class 1 vessels, broken line; Class 2 vessels, solid line.

Figure 4 illustrates the decline in the annual average. The average number of men hooking per effective trip on Class 1 vessels was fairly steady from 1950 to 1955, then dropped and remained at a lower level in 1956–60. The average for Class 2 vessels declined almost steadily from 1950 to 1960. This decrease in the number of men hooking from 1950 to 1960 was not, however, accompanied by a decline in the catch per effective trip. An explanation is given in the section on Apparent Abundance.

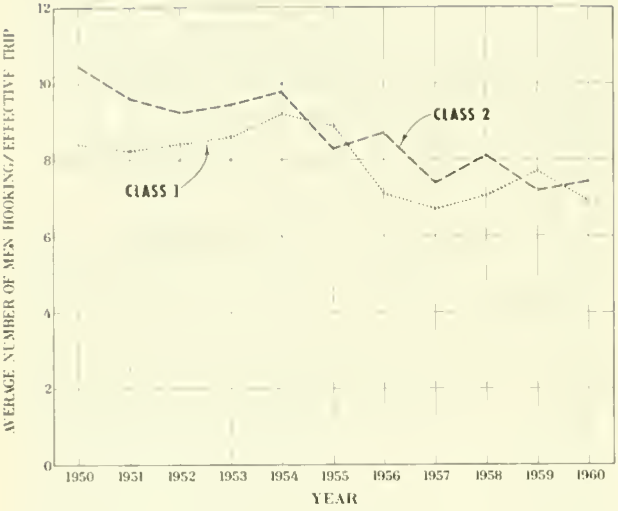

FIGURE 4.— Annual averages of number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60.

DISTRIBUTION OF EFFORT BY AREA

About 80 percent of the effective trips during any given year were in the inshore area (table 7). The percentage of effective inshore trips for both classes of vessels declined from 1952 to 1953. Class 1 vessels showed a further decline in 1954, then a gradual increase, whereas Class 2 vessels showed a gradual increase after 1953 (fig. 5). The percentage of effective inshore trips did not differ greatly between Class 1 and Class 2 vessels. For Class 1 vessels, the percentage of inshore trips, on the average, was 81 percent, whereas for Class 2 vessels, the average was 83 percent over the 11 years.

TABLE 7.—*The number and (in parentheses) percentage of effective trips by Class 1 and Class 2 Hawaiian skipjack tuna vessels in inshore and offshore areas, 1952–62*

Year	Effective trips							
	Class 1 vessels				Class 2 vessels			
	Inshore		Offshore		Inshore		Offshore	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1952	658	(77)	197	(23)	555	(80)	137	(20)
1953	799	(72)	308	(28)	738	(76)	232	(24)
1954	696	(70)	291	(30)	690	(77)	209	(23)
1955	817	(88)	116	(12)	748	(86)	121	(14)
1956	709	(76)	222	(24)	772	(81)	184	(19)
1957	540	(81)	128	(19)	742	(82)	168	(18)
1958	587	(89)	72	(11)	783	(90)	82	(10)
1959	658	(84)	121	(16)	881	(84)	171	(16)
1960	563	(92)	51	(8)	858	(92)	73	(8)
1961	608	(87)	88	(13)	939	(84)	179	(16)
1962	646	(89)	80	(11)	804	(86)	131	(14)
Average [1]	662	(81)	152	(19)	774	(83)	154	(17)

[1] Percentages were computed from the average annual numbers of effective trips.

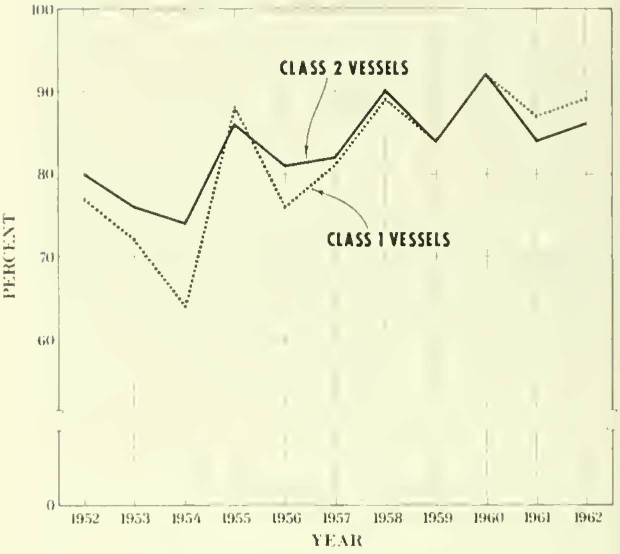

FIGURE 5.—Percentage of effective trips inshore by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

A summary of effective trips by areas for each size class of vessels with respect to poor years and average and good years showed that in poor years, the percentage of effective inshore trips by Class 1 vessels was 84 percent; in average and good years, it was 81 percent. For Class 2 vessels, the values were 86 percent in poor years and 82 percent in average and good years.

One may wonder if skipjack tuna are more abundant inshore, since a larger percentage of the total trips is made within 20 miles from land. Observations of skipjack schools in Hawaiian waters in 1953 indicated that sightings of tuna schools were equally numerous offshore and inshore except for sectors to the northeast and southwest of Oahu (Royce and Otsu, 1955).

If schools are equally abundant offshore and inshore, the question arises as to why effort has been concentrated in the inshore grounds. There are several possible answers. Fishermen reduce costs by remaining close to port as long as they can make profitable catches. The concentration of effort inshore also may be dictated by the quality and quantity of live bait. Even though it may occasionally survive as long as a week, the delicate nehu may die within a few hours. The fishermen logically would fish inshore to use the bait quickly before mortality becomes heavy. Furthermore, the need to replenish live-bait supplies to some extent restricts trips to the distant offshore grounds, where live bait is unavailable.

EFFECTIVE TRIPS BY SIZE CLASSES OF VESSELS

The average number of effective trips per vessel per year fluctuated widely in 1952–62 (table 8). The average number of effective trips per Class 1 vessel per year (fig. 6) fluctuated between 51 and 72 in 1952–58, rose sharply to 97 in 1959, and ranged between 77 and 91 in 1960–62. For Class 2 vessels, the average rose very sharply from 58 to 88 in 1952–53, then declined to 75 in 1954 and to 62 in 1955. After 1955 the average appeared to increase gradually. The reason for the increase in the number of effective trips, particularly the sharp increase since 1959 among Class 1 vessels, is not known.

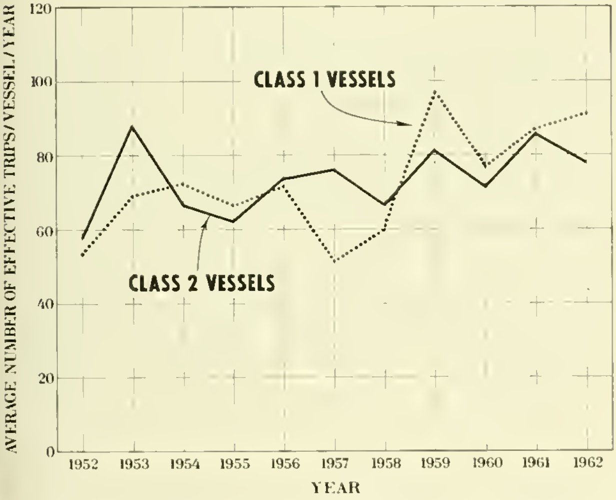

FIGURE 6.—Average number of effective trips per vessel per year by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

TABLE 8.—*The total number of effective trips and the average number of effective trips per vessel by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62*

Year	Class 1 vessels			Class 2 vessels		
	Vessels fished	Total	Average per vessel	Vessels fished	Total	Average per vessel
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1952	16	855	53	12	692	58
1953	16	1,107	69	11	970	88
1954	15	987	66	12	899	75
1955	14	933	67	14	872	62
1956	13	931	72	13	956	74
1957	13	668	51	12	910	76
1958	11	659	60	13	865	66
1959	8	779	97	13	1,055	81
1960	8	614	77	13	931	72
1961	8	696	87	13	1,118	86
1962	8	726	91	12	935	78

APPARENT ABUNDANCE

The catch per unit of effort does not provide estimates of true abundance but of apparent abundance, since it is affected by availability[1] and vulnerability[2] to the fishing gear. In the section that follows, I discuss the catch per effective trip, the factors affecting it, and the method used to obtain a standard unit of effort.

CATCH PER EFFECTIVE TRIP BY SIZE CLASSES OF VESSELS AND AREAS

Data on Y/g (catch per effective trip) by size classes of vessels and areas are given in table 9 and plotted in figure 7. The inshore Y/g for Class 1 vessels fluctuated within a relatively narrow range, whereas that for offshore fishing fluctuated more widely. The curves for Class 1 vessels offshore and Class 2 vessels inshore were similar. Catches of Class 1 vessels that fished offshore fluctuated widely and followed the curve for the total catch. The inshore and offshore Y/g for Class 1 vessels and total catch were significantly correlated ($r = 0.675$; $df = 9$; $p = 0.03$ and $r = 0.923$; $df = 9$; $p < 0.001$, respectively). A similar comparison of data for Class 2 vessels showed that both the inshore and offshore Y/g were sig-

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[1] "Availability is the portion (a percentage) of the recruited population that is physically within the geographic range of the fishery during the fishing season." (Ahlstrom, 1960: p. 1361.)

[2] "Vulnerability is the accessibility of the fish within the geographic range of the fishery to the efforts of a fishery." (Ahlstrom, 1960: p. 1361.)

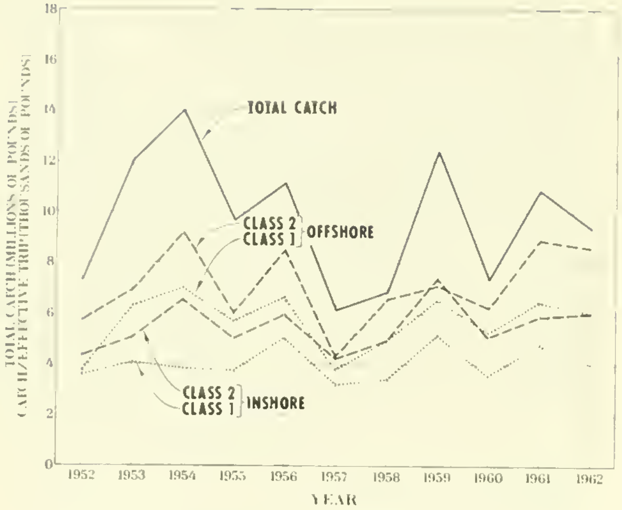

FIGURE 7.—Total catch and catch per effective trip by areas for Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

nificantly correlated with the total catch ($r = 0.762$; $df = 9$; $p<0.01$, and $r = 0.697$; $df = 9$; $p = 0.02$, respectively).

FACTORS AFFECTING ESTIMATES OF THE CATCH PER EFFECTIVE TRIP

Proper interpretation of statistics on catch and effort requires information about factors that contribute to variations in catch per unit of effort. For the skipjack tuna fishery in Hawaii, a number of factors have been isolated as causes of variation in catch per effective trip. Some of these are discussed here.

Changes in the Availability of Skipjack Tuna

In a study on the oceanography and skipjack fishery in the Hawaiian region, Seckel and Waldron (1960) pointed out that the time of initial warming of the surface water at Koko Head, Oahu, appears to be related to the annual skipjack landings. When the initial warming occurred in February, this implied that the California Current System was well developed and average or better-than-average fishing years occurred. When the initial warming occurred in March, fishing was poor.

The relation between the time of initial warming and skipjack landings later in the season appeared to have some predictive value concerning the availability of skipjack tuna. According to Seckel (1963; fig. 4), the initial warming occurred in March in 1952, 1955, 1957, 1958, and 1960; skipjack availability should be low during these years. As was pointed out earlier, however, the catch in 1955 was close to the average catch of 9.7 million pounds for 1952–62 (table 1) and was considered an average year for the purpose of this report. The forecasts made from 1959 to 1962 were dependable, but the prediction of favorable fishing conditions and catch levels could not be made with assurance because only partial understanding of the relation has been achieved. At present, variations in skipjack availability appear to be one of the most important factors causing fluctuations in the total catch of skipjack in the Hawaiian fishery.

Changes in the Number of Men Hooking and in Fishing Technique

Since the average number of men hooking per effective trip declined between 1950 and 1960, I examined the data to see if the Y/g showed a similar decline. The results (table 9 and fig. 7) showed that Y/g did not decline during 1952–62. For example, if the poor years of 1952, 1957, 1958, and 1960 are omitted to simplify the comparison, Y/g for the remaining years appears to be approximately the same before and after 1955, that is, no indication exists of a decline in Y/g. An excellent 2-year comparison is provided by the data of both size classes in 1954 and 1959, in which years

TABLE 9.—*The catch per effective trip of Class 1 and Class 2 Hawaiian skipjack tuna vessels in inshore and offshore areas, 1952–62*

Year	Catch per effective trip			
	Class 1		Class 2	
	Inshore	Offshore	Inshore	Offshore
	Pounds	*Pounds*	*Pounds*	*Pounds*
1952	3,586	3,728	4,323	5,722
1953	4,055	6,337	5,069	6,943
1954	3,867	7,758	6,312	9,210
1955	3,762	5,704	5,048	6,023
1956	4,914	6,338	5,871	8,228
1957	3,219	3,790	4,210	4,333
1958	3,238	4,928	4,723	6,593
1959	5,133	6,551	7,416	7,129
1960	3,573	5,283	5,093	6,244
1961	4,775	6,490	5,891	9,909
1962	4,019	6,071	6,066	8,602

oceanographic conditions were similar. In both years the water in the Hawaiian Islands area warmed early (Seckel and Waldron, 1960); the total catch was above average; and Y/g was also large (table 9) even though the average number of men hooking per effective trip (both classes of vessels) was 9.6 in 1954 and 7.3 in 1959.

Richard S. Shomura (personal communication) has suggested that failure of this decline in Y/g to appear may have been the result of a change in the fishing techniques necessitated by a decrease in the number of skilled fishermen. In the past, when a fisherman caught a fish, he grasped it under his arm so that he could remove the barbless hook; he then dropped the fish on the deck. (Among local fishermen, the method is called "catch" or its Japanese equivalent "daku" which means to hold in one's arm.) A considerable amount of practice and experience is required before one develops the skill necessary to fish by this method. Another method used only occasionally in the past was "flipping," in which the fisherman swings the fish aboard and suddenly relaxes the tension of the pole to permit the hook to fall clear of the fish's mouth before it drops on the deck. (This method is sometimes called "mochikomu" which in Japanese means to bring in.) Interviews with fishermen indicated that flipping allows them to catch fish faster and does not require the same degree of skill as "catching fish under the arm," but the fishermen tire more rapidly. The shift in emphasis from catching under the arm to flipping permitted a short-handed crew of limited experience to equal or better the catch of a larger and more experienced group of fishermen. Because flipping bruisès the fish, some fishermen still catch under the arm when fishing large skipjack, which bring a premium price on the fresh-fish market. Damaged fish bring lower prices.

Changes in the Efficiency of Class 1 Vessels

Fishing efficiency per vessel also increases when vessels that do poorly in the fishery are forced to stop fishing. In 1952–62, the number of Class 1 vessels actively fishing decreased from 16 to 8 (2 were wrecked and 6 stopped fishing). When Class 1 vessels were ranked according to the total catch of each vessel, the results showed that the eight vessels fishing in 1962 were usually among those that were ranked high in previous years. Because those that did poorly stopped fishing, the fishing efficiency (as measured by the average catch per effective trip) of all the remaining vessels increased. This increase in fishing efficiency also may have offset the effect of the decline in the number of men hooking per trip.

The number of Class 2 vessels reached a maximum of 14 in 1955 and declined to 12 in 1962 (1 was wrecked and 1 stopped fishing). Since only one vessel in this size class has stopped fishing, the efficiency of the class could not be expected to change markedly.

Amount of Bait Used per Effective Trip

Bait supply as well as the number of men hooking per effective trip may affect catch. It is important, then, to determine whether the larger vessels do carry and use more bait than the smaller ones. Data on bait catch (table 10) permitted investigation of this problem.

TABLE 10.—*Total buckets of bait used and amount used per effective trip by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62*

Year	Class 1			Class 1		
	Total buckets of bait used	Effective trips	Buckets used per effective trip	Total buckets of bait used	Effective trips	Buckets used per effective trip
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1952	12,202	855	14.3	11,319	692	16.4
1953	12,932	1,107	11.7	14,163	970	14.6
1954	12,592	987	12.8	15,503	899	17.2
1955	13,144	933	14.1	16,092	872	18.4
1956	12,092	931	13.0	14,588	956	15.2
1957	8,187	668	12.2	13,497	910	14.8
1958	5,721	659	8.7	10,966	865	12.7
1959	10,233	779	13.1	17,961	1,055	17.0
1960	5,748	614	9.4	10,593	931	11.4
1961	9,462	696	13.6	18,051	1,118	16.1
1962	9,315	726	12.8	14,733	935	15.8
Average	10,148	814	12.3	14,315	928	15.4

Class 2 vessels used more bait per effective trip in all years for which there were records. The 11-year unweighted averages indicated that Class 1 vessels used 12.3 buckets per effective trip compared with 15.4 buckets per effective trip by Class 2 vessels. The difference in the average number of buckets of bait used per effective trip between class 1 and Class 2 vessels was statistically significant

($t = -11.31$; $df = 10$; $p < 0.001$). We can conclude, therefore, that the amount of bait used in fishing contributed to the larger catch per effective trip among Class 2 vessels.

STANDARDIZATION OF CATCH PER EFFECTIVE TRIP

Differences between the large and the small vessels in numbers of men and in quantity of bait and hence in catching ability can complicate the estimation of apparent abundance. Rather than analyze data for the two classes of vessels separately, I have employed only one index, based on a "standard" unit of fishing effort. This unit is derived from a set of conversion factors which translate unequal fishing practices and capacities into a standard unit. For example, under conditions of equal abundance, when a small vessel makes a smaller catch than a large vessel, standardization of the effort units takes into account the differences in their fishing power. A general discussion of the problems in standardizing fishing effort may be found in Gulland (1955, 1956), in Shimada and Schaefer (1956), and in Schaefer (1963).

Efficiency Factors

The yearly Y/g of the two classes of vessels by areas permits the calculation of efficiency factors (Shimada and Schaefer, 1956). For each area the ratio of the yearly Y/g of Class 1 to that of Class 2 was computed. For example, from table 9, values of Y/g for 1952 were as follows:

Class 1: Inshore —3,586 pounds/effective trip
Offshore—3,728 pounds/effective trip
Class 2: Inshore —4,323 pounds/effective trip
Offshore—5,722 pounds/effective trip

For Class 1 vessels, the efficiency factor for inshore was 3,586/4,323 = 0.83; for offshore, it was 3,728/5,722 = 0.65. The efficiency factors for Class 2 vessels are fixed at 1.00 for all years. The mean efficiency factor for the year is the geometric mean of the inshore and offshore values. The geometric mean is appropriate for averaging ratios.

The mean efficiency factors for Class 1 vessels and the average for the 11-year period not only demonstrate the greater capability of Class 2 vessels, but also the variability of the factor (table 11). For example, if the Y/g of Class 1 vessels were some constant proportion of that for Class 2 vessels, one would expect an almost constant efficiency factor. The efficiency factors of Class 1 vessels, however, were as high as 0.86 and as low as 0.68. These values show no trend, and apparently are not related to good and poor years.

TABLE 11.—*Values of efficiency factors for Class 1 Hawaiian skipjack tuna vessels in terms of a fixed value of 1.00 for Class 2 vessels*

[These factors were used to standardize the unit of effort in 1952-62]

Year	Class 1	Year	Class 1
1952	0.74	1958	0.72
1953	.86	1959	.80
1954	.72	1960	.77
1955	.84	1961	.73
1956	.80	1962	.68
1957	.82	Average	.77

TABLE 12.—*Values of efficiency factors for Class 1 Hawaiian skipjack tuna vessels inshore and offshore and for Class 2 vessels inshore in terms of a fixed value of 1.00 for Class 2 vessels offshore*

Year	Class 1		Class 2
	Inshore	Offshore	Inshore
1952	0.63	0.65	0.76
1953	.58	.91	.73
1954	.42	.84	.68
1955	.62	.95	.84
1956	.60	.77	.71
1957	.74	.87	.97
1958	.49	.75	.72
1959	.72	.92	1.04
1960	.57	.85	.82
1961	.48	.65	.59
1962	.47	.70	.70
Average	.57	.80	.78

The efficiency factors by area (computed in terms of a fixed value of 1.00 for Class 2 vessels, offshore) for each vessel class (table 12) show that the values for both Class 1 and Class 2 were almost consistently smaller for inshore than for offshore fishing. The average for the 11-year period indicates that the offshore values of efficiency factors are higher than their respective inshore values. Furthermore, the mean efficiency factor for Class 1 offshore is slightly larger than that for Class 2 inshore. This result was not unexpected because efficiency factors do not take into account the ability of a vessel to visit distant areas where fish density may be higher. Although it may appear from the values of efficiency factors in table 11 that Class 2 vessels always have better results than Class 1 vessels, the data indicate that, on the average, the offshore catches of Class 1 vessels are likely to be larger than those of Class 2 vessels fishing in inshore waters.

Catch per Standard Effective Trip

The efficiency factors, given in table 11, were used in calculating the standard unit of effort. For example, in 1952 there were 855 effective trips by Class 1 vessels and 692 by Class 2 vessels. The standard effective trip is the sum of the products of the mean efficiency factor and total number of effective trips of the size classes:

$0.74(855) + 1.00(692) = 1{,}325$ standard effective trips. The catch per standard effective trip (Y/f; the notation f refers to fishing effort expressed in standard effective trips) is found by dividing the sample catch by the standard effective trips:

$$\frac{6{,}277{,}046}{1{,}325} = 4{,}737 \text{ pounds per standard effective trip;}$$

and the fishing intensity is obtained from the total catch and Y/f:

$$\frac{7{,}291{,}851}{4{,}737} = 1{,}539 \text{ standard effective trips.}$$

The Y/f reflects only apparent abundance based on the trips on which fish were caught. The total catch of skipjack tuna in pounds, Y/f, and relative effective fishing intensity per Class 2 trip are presented in table 13 and the index curves are illustrated in figure 8.

Table 13.—*Total landings of skipjack tuna in Hawaii, catch per standard effective trip, and relative effective fishing intensity, 1952–62*

Year	Total catch	Catch per standard effective trip (Class 2 trip)	Relative effective fishing intensity (in Class 2 trips)
	Thousand pounds	*Pounds*	*Trips*
1952	7,292	4,737	1,539
1953	12,059	5,486	2,198
1954	14,021	6,983	2,008
1955	9,694	4,986	1,944
1956	11,132	6,430	1,731
1957	6,130	4,166	1,471
1958	6,834	4,850	1,409
1959	12,413	7,119	1,744
1960	7,360	5,062	1,454
1961	10,894	6,629	1,643
1962	9,415	6,358	1,481

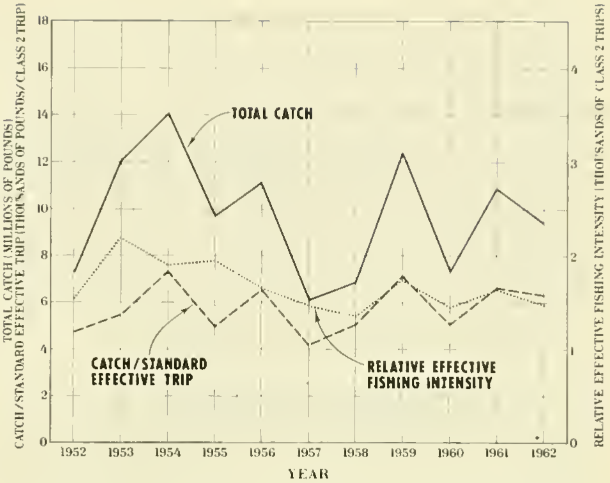

Figure 8.—Total catch, catch per standard effective trip, and the relative effective fishing intensity for skipjack tuna in Hawaii, 1952–62.

The curve for Y/f was at 4,737 pounds in 1952, rose in 1953 and again in 1954 to reach a peak of 6,983 pounds, then dropped to about the 1952 level in 1955. Another peak in 1956 was followed by a decline to its lowest level in 1957. The Y/f reached another peak in 1959, surpassing that of 1954. The Y/f had no trend; rather, the values varied around an average of about 5,700 pounds per standard or Class 2 trip. The relative effective fishing intensity exhibited a slight decreasing trend from about 1953 to 1958 and leveled off at about 1,600 standard trips in 1959–62.

INTERRELATION OF TOTAL CATCH, FISHING INTENSITY, AND APPARENT ABUNDANCE

The catch per standard effective trip (Y/f) and the total catch fluctuated in a similar fashion in 1952–62 ($r = 0.851$; $df = 9$; $p < 0.001$). For the 11-year period, then, the total catch may be used as an index of apparent abundance, but it should by no means be considered an appropriate index in other years. The situation may change in other years, because of the sensitivity of the total landings to various influences such as weather, sea conditions, the amount of effort expended, and the market for skipjack tuna.

The Y/f and the relative effective fishing intensity were not correlated significantly over the 11-year period ($r=0.343$; $df=9$; $p = 0.32$). The lack of correlation suggested that changes in the size of the Y/f were not influenced by changes in the amount of fishing, but by other fishery-independent factors, such as variation in availability and vulnerability; the strength of year classes also may be important (Rothschild, 1965). The effective fishing intensity tended to decline over the years under study, largely because of a decrease in the number of vessels in the fleet.

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CHARACTERISTICS OF THE BLOOD OF ADULT PINK SALMON AT THREE STAGES OF MATURITY

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ABSTRACT

Selected characteristics of the blood of adult pink salmon (*Oncorhynchus gorbuscha*) were studied in fish at three stages of maturity—migrating fish approaching the general area of spawning streams but still in the open ocean, fish in the immediate vicinity of the spawning stream but in the estuary, and fish in the spawning stream. Although some hematological characteristics changed little, blood proteins, glucose, and cholesterol decreased progressively, and lipid phosphorus increased.

The blood chemistry of salmon of the genus Oncorhynchus is especially interesting because of physiological changes that occur during the spawning migration from sea water to estuarine waters of reduced salinity and then into fresh water. This change in the environment is concurrent with the final stages of maturation.

Some information is already available on changes in blood characteristics at this time of the life cycle. Lysaya (1951) found several physiological changes in the blood with advancing sexual maturity in the Asiatic pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*). The erythrocyte count, the hemoglobin concentration, and the blood glucose, chloride, and calcium levels fell; and the erythrocyte sedimentation rate and the blood urea and nonprotein nitrogen concentrations increased. Biologists of the Fisheries Research Board of Canada found that adult sockeye salmon (*O. nerka*) on their spawning migration up the Fraser River lost 11 to 30 percent of their body weight and had decreasing blood cholesterol (Idler and Tsuyuki, 1958); liver glycogen decreased, except for a terminal increase (Chang and Idler, 1960); and concentrations of adrenal corticosteroid hormones increased (Idler, Ronald, and Schmidt, 1959). Chinook salmon (*O. tshawytscha*) during their spawning migration up the Sacramento River and its tributaries in California showed: increased activity of the pituitary with terminal degeneration; hypertrophy of the islets of Langerhans; hyperplasia of the adrenal cortices (a rise in concentration of 17-hydroxycorticosteroids ended with degeneration of the adrenal glands); and the deterioration of the stomach, liver, spleen, thymus, kidneys, thyroid, and cardiovascular system (Robertson and Wexler, 1960, 1962; Robertson, Krupp, Favour, Hane, and Thomas, 1961; Robertson, Wexler, and Miller, 1961; and Robertson, Krupp, Thomas, Favour, Hane, and Wexler, 1961).

In 1963, under the sponsorship of the Bureau of Commercial Fisheries, I had the opportunity to study the hematology and blood chemistry of adult pink salmon in three stages of maturity in Alaska: (1) maturing fish in salt water migrating toward the spawning areas; (2) nearly mature fish milling in the estuary of a small creek; and (3) mature fish spawning in a fresh-water stream. This paper reports the results of these studies.

COLLECTION OF SAMPLES

Pink salmon in the three stages of maturity were taken from three stocks on different dates. Those migrating toward the spawning grounds (termed "migrating"), were taken from the open ocean near the community of Elfin Cove, southeastern Alaska. They were captured on August 5, about a month before

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they would have spawned; only males were sampled. Salmon milling at the mouth of a creek (called "prespawning") were taken August 9, about 2 weeks before the start of movement into fresh water, from a bay at the mouth of a stream at Little Port Walter on the southern end of Baranof Island, southeastern Alaska; equal numbers of males and females were sampled. Salmon spawning in the stream (termed "spawning") were taken from Olsen Creek, which empties into Olsen Bay on Port Gravina, Prince William Sound. They were taken on July 19 (males only) and September 2 (males and females). The Olsen Creek fish, which made up more than half of all the pink salmon sampled, were sampled on two dates because they arrive in two distinct runs. The early run typically lasts from mid-July to mid-August and the late one from late August to middle or late September. These populations may be genetically distinct.

One sample of blood was taken from each specimen while the fish was held on its back, in a wooden trough. A no. 18-½ needle on a syringe was inserted into the dorsal aorta above the roof of the pharynx, in the region of the second gill arch, and 12 ml. of blood were withdrawn. About 0.2 g. (a pinch) of potassium oxalate, an anticoagulant chosen because it is dry and hence does not cause dilution, was placed in the syringe before the sample was taken. The blood was transferred to a capped vial that also contained a pinch of the oxalate and was placed in an iced, insulated chest and transported by plane to the Bureau of Commercial Fisheries Biological Laboratory at Auke Bay. About 24 hours elapsed between collection and analysis of blood.

HEMATOLOGY

Certain hematological characteristics were determined. Specific gravity was measured by standard methods; packed cell volume was estimated after the samples were centrifuged in Wintrobe tubes at 2,700 r.p.m. for 15 minutes; erythrocytes were counted by standard techniques (Wintrobe, 1933) with 0.85 percent saline as a diluent; and hemoglobin was determined with Hycel[1] cyanomethemoglobin reagents. Mean corpuscular volume, mean corpuscular hemoglobin, and mean corpuscular hemoglobin concentration were calculated by the formulas of Wintrobe (1933). A current general reference for work of this type is that of Hesser (1960).

The results of the analyses (table 1) are discussed in comparison with the results of other workers. Because most of the characteristics did not vary among the three stages

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[1] Trade name referred to in this publication does not imply endorsement of commercial product.

TABLE 1.—*Certain hematological characteristics of adult pink salmon in three stages of maturity from three areas of Alaska in 1963*

[Numbers in parentheses are numbers of samples analyzed]

Stages of maturity	Mean specific gravity	Mean packed cell volume	Mean erythrocytes	Mean hemoglobin	Mean corpuscular volume [1]	Mean corpuscular hemoglobin [2]	Mean corpuscular hemoglobin concentration [3]
		Percent	*Number/mm.^{3}×10^6*	*Grams/100 ml.*	μ^3	*Micro micrograms*	*Percent*
Migrating (Elfin Cove)							
Males	1.061(16)	42(15)	0.98(15)	11.3(15)	439(15)	118(15)	27(15)
Prespawning (Little Port Walter)							
Males and females	1.057(15)	38(15)	.97(15)	10.7(15)	396(15)	114(15)	28(15)
Spawning (Olsen Creek)							
Males	1.059(31)	38(29)	1.01(29)	11.1(29)	403(29)	117(29)	30(29)
Females	1.058(8)	32(8)	.94(8)	10.5(8)	354(8)	114(8)	32(8)
Combined [4]							
Mean	1.059(62)	39(59)	.97(59)	11.0(59)	410(59)	116(59)	28(59)
Standard deviation	.004	4.5	.17	.9	69	22	3
Range	1.050-1.065	32-52	0.53-1.35	8.7-13	270-641	84-196	21-38

[1] $\text{MCV}=\frac{\text{Volume of red blood cells in 1,000 ml. blood}}{\text{Red blood cell count in million/mm.}^3}$

[2] $\text{MCH}=\frac{\text{Hemoglobin in grams per 1,000 ml. blood}}{\text{Red blood cell count in million/mm.}^3}$

[3] $\text{MCHC}=\frac{\text{Hemoglobin in grams percent} \times 100}{\text{Packed cell volume}}$

[4] Female pink salmon from Olsen Bay not included.

of maturity, only the mean from each stage and the grand average, range, and standard deviation for the three stages combined are given in table 1. Statistical comparisons were made by the one-way analysis of variance, or F-test (Li, 1957). No distinction is made here between early- and late-run salmon at Olsen Creek.

The specific gravities, erythrocyte counts, and hemoglobin concentrations fall within the ranges of those listed by Wintrobe (1933) for oceanic bony fishes, although the mean corpuscular volume and mean corpuscular hemoglobin were high and are comparable with the more primitive fishes.

In the comparison of my present findings on hematology of pink salmon with those of other workers, several points are of interest. In California, Robertson, Krupp, Favour, Hane, and Thomas (1961) found for chinook salmon that erythrocyte counts, hemoglobin levels, and packed-cell volumes increased during the migration and decreased during the spawning stage (to levels similar to those in animals in the open sea). My findings agree with those of Robertson and his associates in that packed-cell volumes (fig. 1) were higher in migrating males than in spawning males. The packed-cell volumes in combined male and female samples were also higher in prespawning populations than in spawning populations. Within the spawning population, the males had greater packed-cell volumes than the females. A significant increase (at the 2.5-percent level) in mean corpuscular hemoglobin concentration between the prespawning and the spawning stages was concurrent with the small decrease in packed-cell volume.

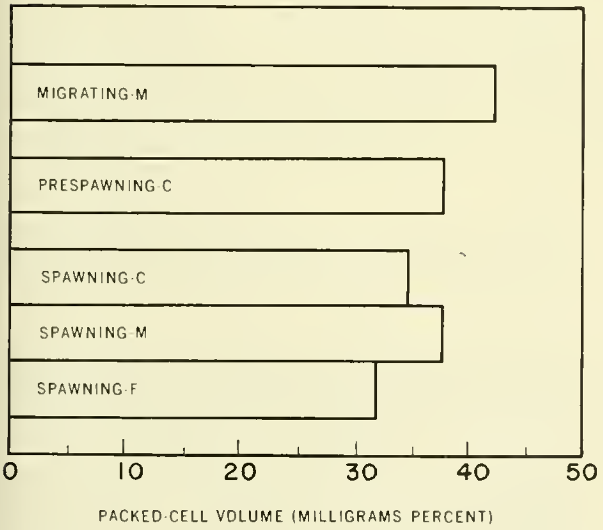

Figure 1.—Packed-cell volume of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males.)

In his studies of pink salmon in Asia, Lysaya (1951) found that erythrocyte counts and hemoglobin levels fell noticeably between the time fish entered the estuary and the time they arrived on the spawning grounds. Such a trend is clearly evidenced by the decrease in packed-cell volume in my study, although it is not noticeable in the erythrocyte and hemoglobin values. The absence of a difference in hemoglobin concentrations between prespawning and spawning stages in my work, was also reported by Sinderman and Mairs (1961) for the alewife, *Alosa pseudoharengus,* a fish that returns to the sea after spawning in fresh water.

Benditt, Morrison, and Irving (1941) found that in Atlantic salmon (*Salmo salar*) affinity of hemoglobin for oxygen was greater while fish were in the spawning stage in fresh water than in the prespawning or migrating stage in salt water. This last phenomenon would compensate those changes mentioned above that would tend to decrease the oxygen-carrying efficiency of the blood. Perhaps an understanding of these points will be possible when larger numbers of fish are analyzed at all stages of migration.

BLOOD CHEMISTRY

The concentrations of several components of blood (table 2) were determined by the techniques given in Fister (1950). As with the hematology and corpuscular indices, the measured values of some of the characteristics of blood did not vary significantly among the three stages of maturity; only the mean from each stage and the mean, range, and standard deviation for the three stages combined are given in table 2.

TABLE 2.—*Average values in blood chemistry of adult pink salmon at three stages of maturity from three areas of Alaska in 1963*

[Numbers in parentheses are numbers of samples analyzed]

Stage of maturity	Albumin [1]	Globulin [1]	Glucose [2]	Cholesterol [1]	Lipid phosphorus [2]	Uric acid [2]	Urea [2]	Creatinine [2]
	Grams percent	*Grams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*
Migrating (Elfin Cove)								
Males	1.5(11)	0.4(12)	101(16)	835(10)		2.2(16)	4.1(15)	1.0(16)
Prespawning (Little Port Walter)								
Males	1.3(8)	.7(8)				1.4(8)	5.1(15)	
Females	.7(8)	1.0(8)				2.1(8)		
Combined			68(16)	656(14)	5.8(11)			
Spawning (Olsen Creek)								
Males	1.8(26)	.6(23)					7.4(23)	1.2(16)
Early run			78(16)	494(16)	15.9(14)	.7(16)		
Late run			43(11)	580(14)	11.3(16)	1.5(16)		
Females								
Late run	.6(5)	.4(5)	41(8)	542(7)	17.5(8)	1.7(5)	6.7(6)	
Combined [3]								
Mean	1.5(53)	.7(51)	75(59)	621(54)	11.0(41)	1.6(64)	5.8(53)	1.1(32)
Standard deviation	.6	.4	30	136	3.3	.5	5.2	.5
Range	.5-3.4	.2-1.2	23-167	364-1,220	2.5-20.5	.3-2.9	.5-28	.3-2.9

[1] Plasma.

[2] Whole blood.

[3] Female pink salmon from Olsen Bay not included in combined values.

ALBUMIN AND GLOBULIN

Albumin and globulin are discussed together because both are blood proteins. Comparisons are made between males and females (table 2) in the three spawning stages (figs. 2 and 3).

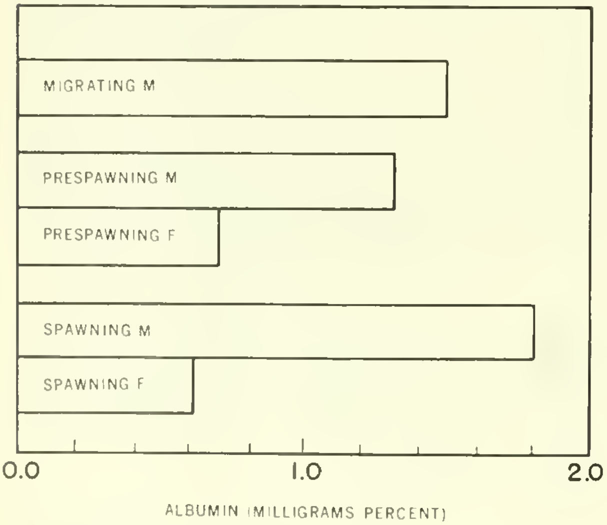

FIGURE 2.—Albumin of blood of adult pink salmon in three stages of maturity. (F, females; M, males.)

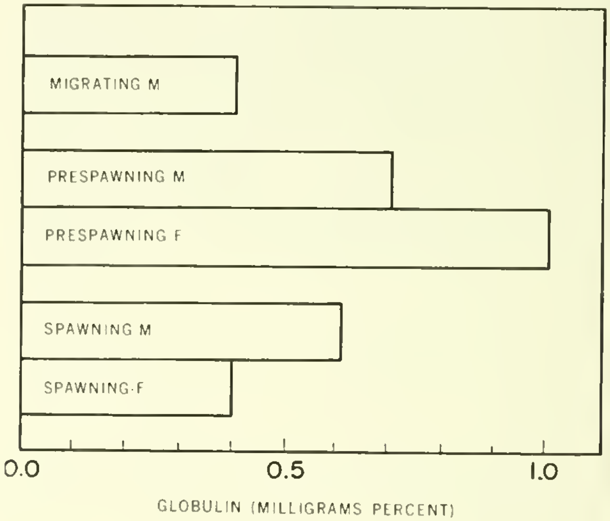

FIGURE 3.—Globulin of blood of adult pink salmon in three stages of maturity. (F, females; M, males.)

Although the range in values was large, the average concentrations of components in males showed little change from the migrating through the prespawning and spawning stages. The albumin-globulin ratio was greater than 1:1—the ratio considered normal for mammals and most fishes (Shell, 1961). The albumin values for prespawning females were about half of those for prespawning males, whereas the globulin values for prespawning females averaged higher than those for males (table 2). The albumin-globulin ratio was 0.7:1 for prespawning females. The globulin was greatly reduced in spawning females, and the albumin-globulin ratio (1.5:1) was more nearly like the ratio for spawning males (3:1). The results of my analysis of albumin and globulin are consistent with those of Robertson, Krupp, Favour, Hane, and Thomas (1961), who found that the normal ratio of albumin to globulin of 1:2 in chinook salmon living in the sea was reversed in both sexes during migration but tended to revert to the original during spawning.

The greater reduction of albumin and globulin in females than in males by spawning time probably indicates a greater depletion of body protein in egg formation. Shell (1961), who surveyed the nutritive, osmotic, and other functions of blood proteins in fish, found a cyclic reversal of the albumin-globulin ratio in smallmouth bass, *Micropterus dolomieui*, and in his review of the literature stated that "Results of determinations of the A:G ratio in fish are confusing."

GLUCOSE

My discussion of glucose levels includes comparisons between pink salmon in the migrating and the prespawning stages and between pink salmon in early and late runs (fig. 4 and table 2). The drop in glucose between the migrating and prespawning fish is significant at the 1-percent level, and the decrease from early to late spawners is significant at the 2.5-percent level. The different levels of glucose in spawning salmon may be attributed to the fact that the salmon of the early run at Olsen Creek were not completely ready to spawn, whereas the fish of the late run were actually spawning. The findings are in accord with those of Lysaya (1951).

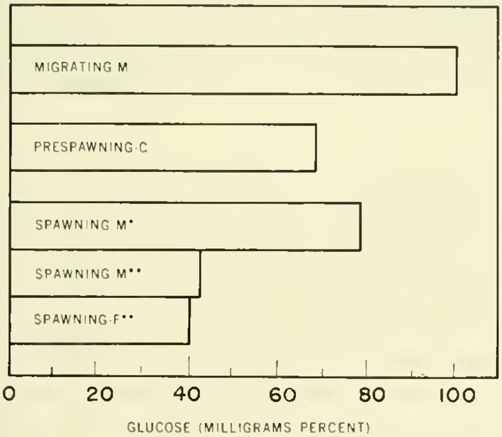

FIGURE 4.—Glucose of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

It is commonly assumed that carbohydrate metabolism in fish is inefficient. Robertson and Wexler (1960), however, found an increase in the number and size of islets of Langerhans in chinook salmon during the spawning migration. Robertson, Krupp, Favour, Hane, and Thomas (1961) found an increase in blood glucose while fish were migrating from the open sea, followed by a tendency toward a decrease during spawning. They suggested that rising levels of blood glucose are due to gluconeogenesis that results from the action of increasing adrenal corticoids on muscle and fat deposits and a simultaneous increase in insulin production to utilize the product.

This viewpoint is somewhat corroborated by studies on the Fraser River in which sockeye salmon have shown an 11- to 30-percent loss of body flesh (Idler and Tsuyuki, 1958) accompanying increased production of adrenal corticosteroid hormones (Idler et al., 1959). Chang and Idler (1960) observed that liver glycogen gradually decreased during migration in fresh water but increased at spawning. These changing glycogen levels were attributed to changing hormone balances.

CHOLESTEROL

Cholesterol levels are compared among the three stages of maturity (fig 5). A downward trend in cholesterol levels from the migrating to the spawning stage was consistent, i.e. significantly lower (at the 1-percent level) in the prespawning than the migrating fish and in the spawning than the prespawning fish. Robertson, Krupp, Favour, Hane, and Thomas (1961) and Idler and Tsuyuki (1958) observed this same consistent downward trend in chinook salmon. Although I found this downward trend in cholesterol levels from the migrating to the spawning stage, levels in pink salmon within the spawning group were higher in the late run than in the early run.

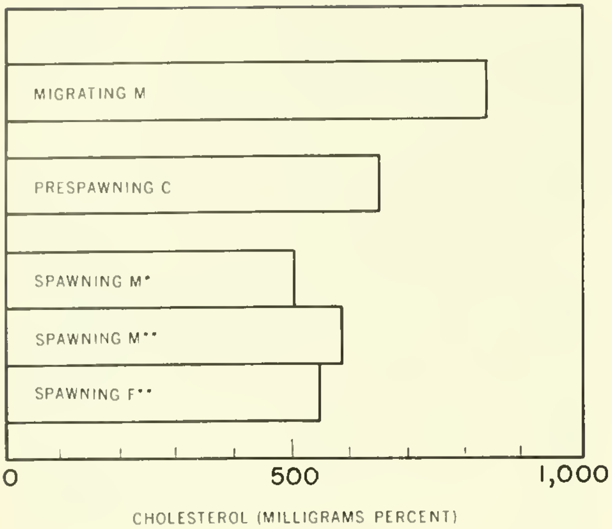

Figure 5.—Cholesterol of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

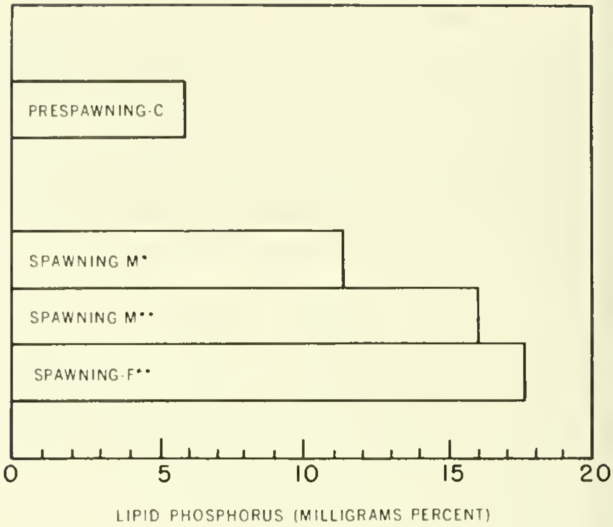

Figure 6.—Lipid phosphorus of blood of adult pink salmon in two stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

The function of cholesterol in the metabolism of fishes (reviewed by Shell, 1961) remains obscure. In my study, however, cholesterol showed an inverse correlation with lipid phosphorus (significant at the 1-percent level).

LIPID PHOSPHORUS

Concentrations of lipid phosphorus in samples from the prespawning and spawning stages and the early and late spawning runs are compared (fig. 6). No data are available from the migrating group. The increase in lipid phosphorus levels from the prespawning to the spawning stage was significant at the 1-percent level. The values for males in the spawning stage in the early part of the run (fig. 6) were also significantly higher than in the late run (at the 1-percent level.) The high values for lipid phosphorus in the females sampled in the late run may be due to a terminal increase in 17-hydroxycorticosteroids in females as values at that time are dropping in males (Hane and Robertson, 1959). Although Shell (1961) found a direct correlation between lipid phosphorus and the blood proteins (albumin and globulin), no such correlation is evident in my data. Comparisons between individual animals, however, indicated a positive correlation (1-percent level of significance) with glucose. The results suggest a mechanism whereby the concentration of lipid phosphorus increases as cholesterol and glucose decrease.

URIC ACID

The values for uric acid are discussed for males and females in the three stages of maturity. The decline in uric acid concentration in the blood of males from the migrating to the prespawning stage is significant at the 1-percent level (fig. 7). The further drop in uric acid from the prespawning to the early part of the spawning stage (in the early run only) is also significant at the 1-percent level. No such drop is apparent, however, in the comparison of the males of the prespawning and the late part of the spawning stage (fig. 7). Within the prespawning stage, uric acid values were higher in the females than in the males (significant at the 5-percent level). Uric acid concentrations in females from the late spawning stage average only slightly higher than those in the males (table 2). If uric acid is accepted

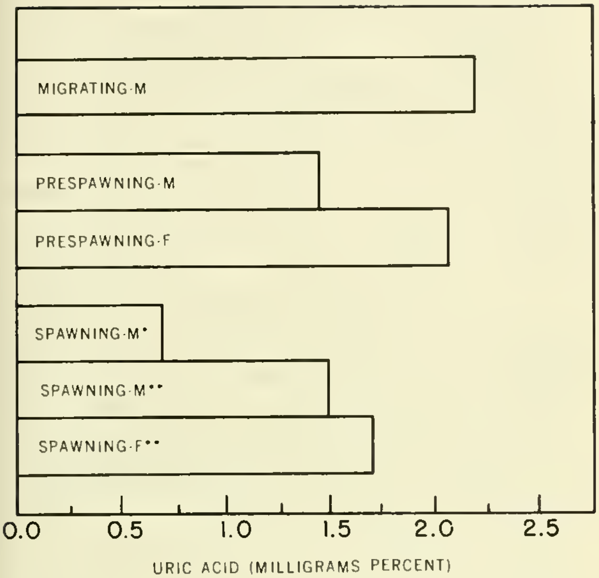

Figure 7.—Uric acid of blood of adult pink salmon in three stages of maturity. (F, females; M, males; single asterisk, early run; double asterisk, late run.)

as an end product of purine metabolism, a decline in purine metabolism at spawning is indicated, and females maintain a higher level longer than males.

UREA

The variations in the concentration of urea among individual specimens from an area were so great that no trend is apparent for this blood component, which is the end product of nitrogen metabolism. Lysaya (1951) noted increasing concentrations as spawning approached and attributed death of pink and chum salmon to urea poisoning.

CREATININE

No data are available on the concentrations of creatinine in blood samples from fish in the prespawning stage, and no trend is indicated by the values for the other groups. Creatinine is sometimes considered an end product of tissue catabolism, which is a dominant process in the fish sampled here. The values I found, however (table 2), are similar to those determined for smallmouth bass by Shell (1961) and for carp (*Cyprinus carpio*) and brook trout (*Salvelinus fontinalis*) by Field, Elvehjem, and Juday (1943) for fish in which catabolism was not high.

SUMMARY AND CONCLUSIONS

Blood samples were taken from adult pink salmon collected at three stages of maturation during their migration to the spawning grounds—in the ocean actively migrating, milling in the estuary of a spawning stream, and in fresh water on the spawning grounds.

Basic hematological characteristics, including specific gravity, packed-cell volume, erythrocytes, hemoglobin, corpuscular volume, corpuscular hemoglobin, and corpuscular hemoglobin concentration, were determined. Statistical analyses indicated no significant difference among groups of fish.

The concentrations of several components of blood indicate that several changes accompany migration and maturation. As pink salmon mature, utilization of protein reserves (evidenced by lowered albumin and globulin levels in females) may result from rapid building of egg tissue. Glucose levels declined, especially in females. Cholesterol concentrations also declined, although lipid phosphorus rose in both sexes; the increase was especially noticeable in females. Lipid phosphorus may play an increasingly important part in energy transfer as salmon mature.

The pink salmon from the spawning stream were from two distinct components of the run—the early and the late. The late spawners had significantly higher concentrations of cholesterol and uric acid, but lower levels of glucose and lipid phosphorus. I do not know if these differences are due to intrinsic genetic factors or are induced by extrinsic environmental factors.

I could see no trend in urea or creatinine concentrations at the three stages of maturity.

ACKNOWLEDGMENTS

David Boye and Mrs. Frances Pierce helped with the statistical comparisons. Theodore R. Merrell, Jr., and several other staff members at the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, aided in collecting samples. This work was financed by the Bureau of Commercial Fisheries under Contract No. 14-17-0005-46 with funds made available under the Act of July 1, 1954 (68 Stat. 376) commonly known as the Saltonstall-Kennedy Act.

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CROSS-REACTIVE PROPERTIES OF ANTISERA PREPARED IN RABBITS BY STIMULATIONS WITH TELEOST VITELLINS

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ABSTRACT

Antisera were prepared by injecting rabbits with egg or serum vitellin preparations from seven teleost species belonging to different families. The ranges of reactivity of these antisera were tested with sera from mature females of nine teleost families as well as with sera from females of spiny dogfish, Pacific lamprey, and white sturgeon. All of these antisera reacted with vitellins from all species tested from the homologous families. Antisera prepared against rockfish and flounder vitellins cross-reacted with sera from mature females of all teleost species tested. A greater antigenic complexity in the vitellins of more taxonomically advanced species than more primitive species is indicated by the results of the reactions and absorption tests. The results are of practical importance in studies on maturity of fishes and have theoretical implications in the field of systematics.

Fishery researchers have used serological techniques with increasing frequency since 1950. Much of the work has been directed toward identification of populations either through blood-grouping techniques or studies of variable serum antigens (Cushing, 1964). Ridgway, Klontz, and Matsumoto (1962) observed a characteristic antigen in the serum of maturing and mature female sockeye salmon (*Oncorhynchus nerka*). A review of the literature and subsequent studies by our group has revealed that similar components occur not only in all the teleosts but also in all vertebrate classes were oviparity occurs (Urist and Schjeide, 1961; Drilhon and Fine, 1963). These antigens appear to have considerable practical value in investigations of maturity in female fish because of their connection with the process of sexual maturation (Ho and Vanstone, 1961; Olivereau and Ridgway, 1962; Ridgway, 1964; Utter and Ridgway, 1966).

The function of the blood serum as a transporting medium between the site of synthesis in the liver and the site of storage in the ovary appears to explain the presence of yolk components in the blood (Vanstone, Maw, and Common, 1955). The serum vitellins studied have displayed similar biochemical properties, are characterized as phospholipoproteins, and conform to the classical description of avian vitellin as the water-insoluble fraction of the egg yolk (Jukes and Kay, 1932; Vanstone, Maw, and Common, 1955).

This report is based on data obtained through testing numerous antisera for cross-reactive properties. The antisera were prepared in rabbits against vitellins of teleosts. We intend to bring out points of both practical significance and theoretical interest.

METHODS AND MATERIALS

IMMUNOLOGICAL TESTS

A microslide adaptation of the double diffusion method of Ouchterlony as modified by Ridgway, Klontz, and Matsumoto (1962) was used for all serological tests. The agar medium consisted of 1.5 percent Difco agar, 0.72 percent sodium chloride, 0.60 percent sodium citrate, 0.01 percent merthiolate, and 0.01 percent trypan blue. Wells were punched in the agar at 8-mm. intervals and filled to a volume of about 0.01 cc. of reactant. Slides were evaluated after 24 hours of incubation at 37° C.

PRODUCTION OF ANTISERA

Table 1 lists the antisera used in this study. Egg vitellin preparations were made by blending and centrifuging one part eggs with three

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Table 1.—*Antisera used in this study*

Designation	Vitellin source	Number of rabbits
Anti-CLM	Pacific herring (*Clupea harengus pallasi*) eggs	1
Anti-SM	Chinook salmon (*Oncorhynchus tshawytscha*) eggs	3
Anti-CM	Northern squawfish (*Ptychocheilus oregonensis*) eggs.	1
Anti-GM	Pacific cod (*Gadus macrocephalus*) serum	1
Anti-TM	Yellowfin tuna (*Thunnus albacares*) eggs	1
Anti-RM	Copper rockfish (*Sebastodes caurinus*) eggs	3
Anti-HM	Starry flounder (*Platichthys stellatus*) eggs	5

parts 1 percent saline in a Waring Blender.[2] After centrifugation, the addition of 11 parts of distilled water precipitated the vitellins from the supernatant fluid. The precipitate was dissolved again in saline, reprecipitated and redissolved, and used for injections. Whole serum from a mature female Pacific cod was used to produce the anticod vitellin reagent. The resulting antiserum was absorbed at a 1:1 ratio with male cod serum before testing. Usually the vitellin-bearing materials were suspended in a bayol-arlacel mixture and injected into the rabbits intraperitioneally. Consistently uniform results were obtained when other injection procedures were used, but a greater number of injections was usually required. Single bleedings were used for testing with the exception of the reagent prepared against starry flounder vitellin which was a pool of numerous bleedings from five rabbits. The antisera produced in different rabbits injected with the same vitellin material were qualitatively very similar. This uniformity of reagent indicates that the differences reported later are not due to variations in the immune response of individual rabbits.

COLLECTION OF SERUM SAMPLES

Samples of fish serum were taken from whole blood that had been processed within 48 hours after collection; the samples were then stored at -35° C., a temperature at which the vitellin fraction appeared to be stable. Some sera had been stored as long as 8 years when tested.

REACTIVE PROPERTIES OF THE ANTISERA AND VITELLINS TESTED

Table 2 summarizes the data obtained through testing of sera from mature females of various fish species. All antisera were tested with the same fish sera; this testing included males as well as females from most species. The only reaction with male serum occurred between the antirockfish reagent and male rockfish serum. This reaction was very weak and was most likely the result of nonvitellin antigens present in the injected material. The reaction with male rockfish sera could not be confused with the reaction with female rockfish sera.

Table 2.—*Cross-reactivity of rabbit antiteleost vitellin sera with vitellins of fish representing various taxonomic groups* [1]

[X = strong reaction; W = weak reaction; 0 = no reaction]

Reagent	Nonteleosts			Teleosts								
	Agnatha (1)	Chondrichthys (2)	Chondrostei (3)	Clupeid (4)	Salmonid (5)	Cyprinoid (6)	Gadid (7)	Scombrid (8)	Scorpaenid (9)	Cottid (10)	Pleuronectid (11)	Batrachoidid (12)
Anti-												
Clupeid (CLM)	0	0	0	X	0	0	0	0	W	0	0	0
Salmonid (SM)	0	0	0	0	X	0	0	0	W	0	0	0
Cyprinid (CM)	0	0	X	0	W	X	0	0	0	0	0	0
Gadid (GM)	0	0	0	0	0	0	X	W	0	0	0	0
Scombrid (TM)	0	0	0	W	W	W	X	X	X	X	X	0
Scorpaenid (RM)	0	0	X	X	X	X	X	X	X	X	X	X
Pleuronectid (HM)	0	0	0	X	X	X	X	X	X	X	X	X

[1] (1) Pacific lamprey, *Lampetra tridentata*; (2) spiny dogfish, *Squalus acanthias*; (3) White sturgeon, *Acipenser transmontanus*; (4) shad, *Alosa sapidissima*; Pacific herring, *Clupea harengus pallasi*; (5) sockeye salmon, *Oncorhynchus nerka*; (6) carp, *Cyprinus carpio*; northern squawfish *Ptychocheilus oregonensis*; largescale sucker, *Catostomus macrocheilus*; (7) Pacific hake, *Merluccius productus*; Pacific cod, *Gadus macrocephalus*; (8) bigeye tuna, *Thunnus obesus*; Pacific mackerel, *Scomber japonicus*; (9) copper rockfish, *Sebastodes caurinus*; (10) cabezon, *Scorpaenichthys marmoratus*; staghorn sculpin, *Leptocottus armatus*; (11) sand sole, *Psettichthys melanostictus*; English sole, *Parophrys vetulus*; starry flounder, *Platichthys stellatus*; (12) northern midshipman, *Porichthys notatus*.

All antisera reacted strongly with sera from mature females within the families that provided the vitellin for antibody stimulation. Because of this high degree of cross-reactivity within families, the reactions of the antisera may be considered mainly with regard to the family rather than the species from which the vitellin used for antibody stimulation originated. The arbitrary designations given in tables 1 and 2 refer to vitellin of any species of that family.

Four of the reagents also reacted strongly beyond the immediate family group; two of them reacted distinctly with sera from mature females of all teleost species tested. Figure 1 illustrates the reactions of sera from mature female teleosts of six different families when tested with the anti-RM reagent. The strongest reaction was with the female rockfish serum. The degree of cross-reactivity regularly decreased through the somewhat distantly related salmonoids and cyprinoids. Even in these groups, however, the reaction was clear.

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

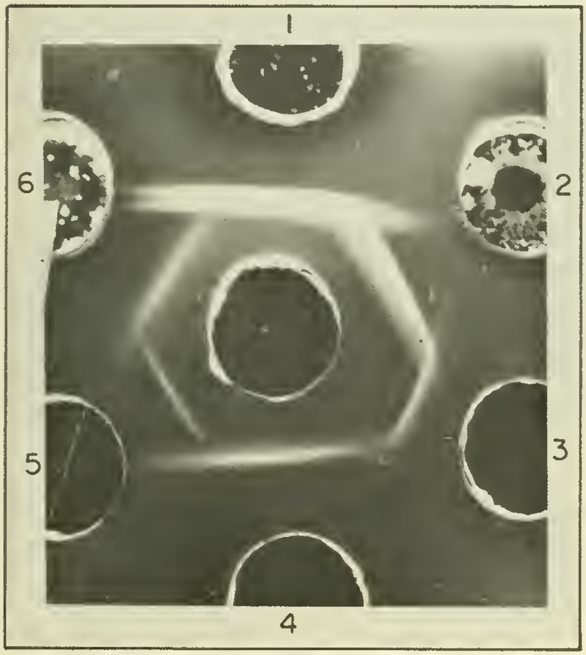

FIGURE 1.—Reactions of sera from mature females of six teleost species with rabbit anti-RM serum. Peripheral wells contain sera from 1, copper rockfish; 2, sand sole; 3, bigeye tuna; 4, Pacific cod; 5, carp; 6, sockeye salmon.

Table 3 gives the results of absorptions of the anti-RM reagent with the fish sera of figure 1. It is evident from both figure 1 and table 3 that the anti-RM reagent contains antibodies of numerous specificities.

Figure 2 presents a more detailed examination of the relationship between SM and RM vitellins. It is evident from figure 2a that the RM vitellin has at least three distinct components. The SM vitellin cross-reacts completely with the antibodies directed against one of these components. Two components are visible in figure 2b that react with the anti-SM antiserum. The RM vitellin cross-reacts partially and very weakly with the antibodies directed against one of these components.

TABLE 3.—*Results of absorptions of rabbit antirockfish vitellin (RM) serum with sera of mature female teleosts*

[X=strong reaction; W=weak reaction; 0=no reaction. See figure 1]

Fish sera used for absorption	Fish sera tested					
	Rockfish	Sole	Tuna	Cod	Carp	Salmon
Unabsorbed	X	X	X	X	X	X
Rockfish	0	0	0	0	0	0
Sole	X	0	W	0	0	0
Tuna	X	0	0	0	0	0
Cod	X	X	X	0	0	0
Carp	X	X	X	X	0	X
Salmon	X	X	X	X	0	0

Comparisons similar to those presented in figure 2 were made between the broadly cross-reactive antisera (anti-RM and anti-HM), the less cross-reactive antisera (anti-CLM, anti-SM, anti-CM, and anti-GM), and the corresponding vitellins. All results were similar. The weak or negative reactions of the RM and HM vitellins with the less cross-reactive or group-specific antisera contrasted with the strong reactions of the anti-RM and anti-HM antisera with the vitellins which elicited the less cross-reactive antisera present an interesting serological phenomenon. The cross-reactive antibodies of the anti-RM and anti-HM antisera apjear to have a considerably greater avidity for the vitellins which elicit group-specific antisera than the group-specific antibodies have for the RM and HM vitellins.

Both the homologous and cross-reaching heterologous antisera gave uniform results where tested with a larger number of individuals. Randomly selected sera from 48 sockeye salmon were tested with anto-SM, anti-RM, and anti-HM reagents; 48 halibut sera were tested with the anti-RM and anti-HM reagents. Results were identical regardless of the antiserum used, including two weak but positively reacting halibut sera.

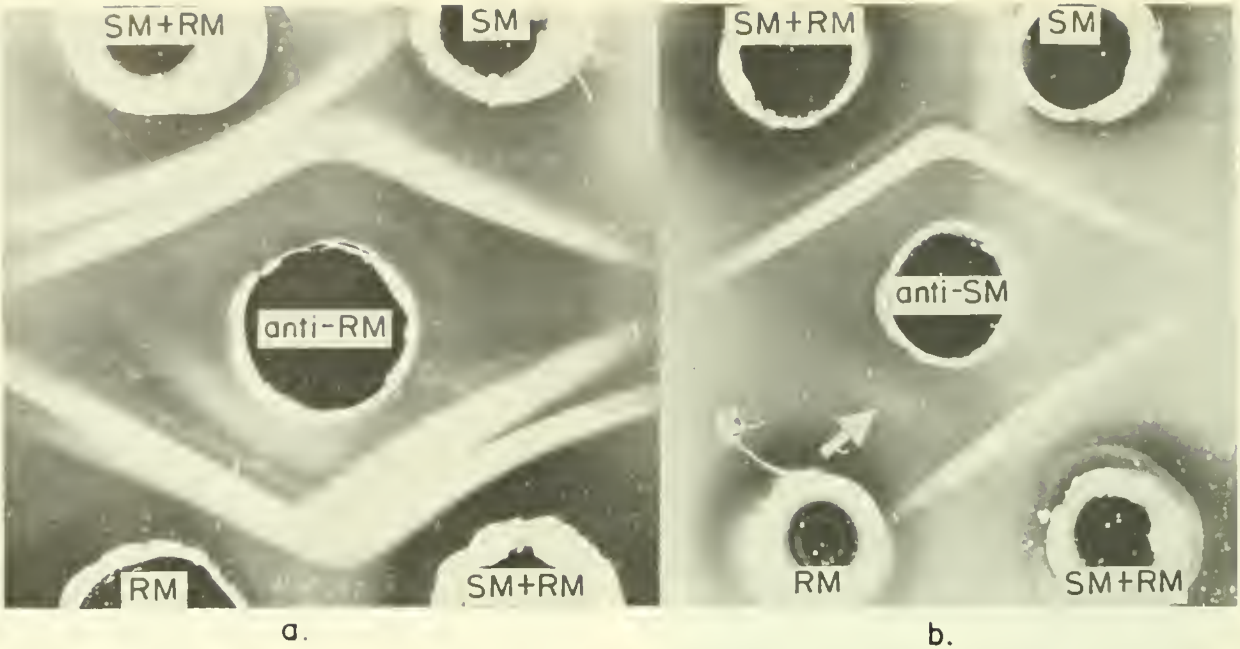

FIGURE 2.—The relation between SM and RM vitellins detected (a) by rabbit anti-RM serum and (b) by rabbit anti-SM serum. Arrow in (b) indicates the partial cross reaction between RM vitellin and the anti-SM reagent.

PRACTICAL APPLICATIONS FOR STUDIES OF MATURITY

The broad cross-reactive range of antisera produced against the vitellins of rockfish and starry flounder is of practical importance. It is likely that these reagents react with serum vitellins from mature female teleosts at least through the taxonomic range of this study. An investigator wishing to include serological data in maturity studies may therefore use a single reagent throughout a range of teleost species rather than produce different antisera for relatively limited taxonomic groupings. The necessity of obtaining vitellin-bearing material for immunizations from species where such materials would be difficult to obtain or process is also eliminated.

The data suggest that vitellins of the most taxonomically advanced species stimulate the highly cross-reactive antisera. Some theoretical implications of this apparent trend are discussed below. As a practical consideration, however, it appears that vitellin from Perciform or closely allied species may be most likely to stimulate antisera which have broad cross-reactive properties.

SYSTEMATIC CONSIDERATIONS

Nuttall (1904) in an early immunological study, observed that the quantities of precipitates formed by specific antigen-antibody interactions decrease as the taxonomic relationships become more distant from the materials used in antibody stimulation. The present study agrees generally with this observation. As illustrated by figure 1, the broadly cross-reactive antisera reacted most strongly with the homologous vitellin and least strongly with the most distantly related cpyrinid and salmonid vitellins. A notable exception is the reaction of sturgeon vitellin with anti-cyprinid vitellin, an antiserum which fails to react with vitellins of numerous, more closely related, groups. The other exceptions include the weak cross-reactions of antisalmonid vitellin with rockfish vitellin but not with herring or carp vitellin, and the similarly weak cross-reaction of anti-clupeid vitellin with rockfish vitellin but not with salmon vitellin.

Fine, Buffa, and Drilhon (1964) found a component in mature female marine lampreys analogous to the teleost vitellins described in this report. The spiny dogfish egg, unlike those of many sharks, is provided with an abundance of yolk material. A Saline extract of the dogfish yolk material was tested in addition to the sera from numerous adult dogfish; this extract also failed to react with any of the antisera used in this study. The lack of reactivity observed here with yolk materials from females of dogfish or lampreys appears to reflect the phylogenetic gap between the teleosts and these more primitive vertebrates.

The vitellin substances of the advanced teleosts that stimulate production of the broadly cross-reactive antisera appears to be biochemically and antigenically more complex than those of the more primitive teleosts. It is evident from figure 1 and table 3 that only a small fraction of the total number of anti-RM antibodies react with SM vitellin; the major antigenic vitellin component of SM is detected, however, by the anti-RM reagent (Figure 2). Possibly the vitellin antigens of more primitive teleost species have been retained in certain advanced species without extensive modification during the evolution of additional vitellin substances.

This study further demonstrates the usefulness of serological methods to determine maturity in oviparous vertebrates. The results are also of significance in systematics. The existence of antigens in the sera of maturing females which do not occur in the sera of males and immature females must be taken into account in studies that attempt to apply serology to problems of taxonomy. These antigens themselves, as was demonstrated here, also offer additional materials for more detailed examinations of systematic relationships.

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OCCURRENCE OF MACROZOOPLANKTON IN TAMPA BAY, FLORIDA, AND THE ADJACENT GULF OF MEXICO[1]

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ABSTRACT

This report describes a 12-month (September 1961 through August 1962) study. Plankton was collected at 14 locations with a No. 000, one-half meter net, which strained an estimated 35 m.^{3} of water per tow. Wet plankton volumes varied from $<$ 0.5 to 92.0 ml. and averaged 7.0 ml. per tow. Fifty-two percent (by volume) of the plankton was collected in the summer, 25 percent in the fall, 18 percent in the spring, and 5 percent in the winter. *Lucifer faxoni,* the most numerous organism, accounted for 18.5 percent of the total plankton volume.

Sixteen species, 24 genera, 30 families, and 21 taxonomic categories higher than family were identified. Decapod crustaceans accounted for 87 percent of the total number of zooplankters collected. The most numerous organisms, in descending order were *Lucifer faxoni,* larval porcellanids, brachyurans, chaetognaths, copepods, larval polychaetes, carideans, appendicularids, larval fish, fish eggs, thallassinids, cladocerans, and larval stomatopods. Larval forms of commercially important species were *Penaeus duorarum, Brevoortia* spp., *Anchoa* sp., *Trachinotus* spp., *Leiostomus xanthurus, Cynoscion* spp., and Soleidae.

Observed temperature ranged from 12.8° to 32.0° C. and salinity from 19.00 to 36.00 p.p.t. In relating the abundance of zooplankton to temperature and salinity the data suggested that low temperatures and salinity values were more restrictive than high ones to most of the organisms.

A study of macrozooplankton was undertaken as part of an investigation of estuarine biology in the eastern Gulf of Mexico. The primary aim was to determine temporal and spatial variations in the abundance of macrozooplankton in the surface waters of Tampa Bay and the adjacent Gulf of Mexico, and to relate the occurrence of frequently collected taxa to water temperature and salinity.

The abundance and composition of zooplankton provide an important index of biological production in estuaries, because zooplankters are the basic food of many marine organisms. Mysids, euphausids, amphipods, larval stomatopods, and fish larvae are frequent in stomachs of commercially important fishes (King, 1954). The bulk of this plankton, however, reaches large fish indirectly through their consumption of foraging organisms.

The literature on zooplankton in the coastal waters of west Florida is limited. No reports deal with the seasonal composition of zooplankton throughout Tampa Bay. Published material includes: a description of certain biological, taxonomic, and ecological aspects of the chaetognaths of the west coast of Florida (Pierce, 1951); notes on chaetognaths from the Gulf of Mexico (Tokioka, 1955); the seasonal distribution of penaeid larvae from the lower portion of Tampa Bay, Fla., and the adjacent Gulf of Mexico waters (Eldred, Williams, Martin, and Joyce, 1965); a qualitative and quantitative seasonal study of the copepods of Alligator Harbor (Grice, 1956); studies of the taxonomy of several calanoid copepods in the eastern Gulf of Mexico (Fleminger, 1957a and 1957b); a preliminary report on the plankton of the west coast of Florida with a discussion of the distribution and occurrence of copepods and other crustaceans (King, 1949); and records of various taxa from the marine and brackish waters of south Florida (Davis, 1947, 1948, 1949, 1950; Davis and Williams, 1950; and Dragovich, 1963).

DESCRIPTION OF THE AREA

Tampa Bay is a shallow embayment consisting of five sub-areas, also identified as bays—

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[1] Contribution No. 27, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.

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Old Tampa Bay, Hillsborough Bay, Tampa Bay, Boca Ciega Bay, and Terra Ceia Bay. Collectively, these areas have a shoreline of 341 km. and cover an area of 896 km.^{2}, 90 percent of which is less than 6.7 m. deep (Olson and Morrill, 1955).[2] The principal tributaries of Tampa Bay are the Hillsborough, Alafia, Manatee, and Little Manatee Rivers. Their discharge is largely influenced by rainfall (Dragovich and May, 1962) and is subordinate to tidal exchange in the circulation of Bay water (Goodell and Gorsline, 1961).

The climate of the Bay area is subtropical. The mean monthly air temperature at Tampa, Fla., averages 22.3° C. annually and varies from 16.2° C. (January) to 27.8° C. (August)[3]. The rainy season in the Tampa Bay area usually extends from June to October. Mean rainfall varies monthly from 3.7 cm. (November) to 21.9 cm. (July) and totals 131.0 cm. annually.

APPARATUS AND METHODS

FIELD PROCEDURES

Plankton was sampled monthly in Tampa Bay and adjacent waters of the Gulf of Mexico from September 1961 through August 1962 (table 1). Surface samples were collected at 14 stations (fig. 1 and table 2) with a No. 000, ½-m., nylon plankton net (mesh size 1.024 mm.). This net was selected primarily for the collection of larval fishes and invertebrates. Tows were made at 5.6 km. per hour (3 knots) for 2 minutes and randomly with respect to tidal stage. Vessel speed was determined before sampling by clocking elapsed time over a known distance. Net-towing rates were held

TABLE 2.—*Sampling locations in Tampa Bay and the adjacent Gulf of Mexico, September 1961–August 1962*

Station	Latitude N.	Longitude W.	Area description
1	27°35.8′	82°57.1′	10 miles (18.5 km.) offshore
2	27°36.0′	82°50.0′	3½ miles (6.5 km.) offshore
3	27°35.5′	82°45.5′	Egmont Key
4	27°32.7′	82°43.7′	Lower Tampa Bay
5	27°38.8′	82°42.7′	Boca Ciega Bay
6	27°41.5′	82°44.1′	Boca Ciega Bay
7	27°42.2′	82°40.5′	Boca Ciega Bay
8	27°33.0′	82°35.7′	Terra Ceia Bay
9	27°41.3′	82°32.9′	Central Tampa Bay
10	27°47.6′	82°34.4′	Upper Tampa Bay
11	27°56.6′	82°37.0′	Central Old Tampa Bay
12	28°00.9′	82°40.7′	Upper Old Tampa Bay
13	27°48.7′	82°26.8′	Lower Hillsborough Bay
14	27°53.7′	82°26.4′	Upper Hillsborough Bay

TABLE 1.—*Dates and numbers of plankton tows in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Dates	Stations														All stations
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
	Number of plankton tows														
Fall															
Sept. 18–27, 1961	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Oct. 2–30	1	1	1	1	2	2	2	1	1	1	1	1	1	1	17
Nov. 1–30	2	2	2	1	2	2	2	2	2	2	2	3	2	2	28
Season total	4	4	4	3	5	5	5	4	4	4	4	5	4	4	59
Winter															
Dec. 11–12, 1961	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
Jan. 8–26, 1962	2	2	2	2	2	2	2	2	1	2	2	2	1	1	25
Feb. 5–10	0	0	0	0	2	2	2	0	0	1	1	2	1	1	12
Season total	4	4	4	4	6	6	6	4	3	5	5	6	4	4	65
Spring															
Mar. 8–29, 1962	1	1	1	1	2	2	2	1	1	1	1	2	1	1	18
Apr. 9–26	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
May 7–29	1	1	1	1	2	1	2	1	2	2	2	1	2	2	21
Season total	4	4	4	4	6	5	6	4	5	5	5	5	5	5	67
Summer															
Jun. 11–28, 1962	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
Jul. 9–25	2	2	2	2	2	2	2	1	2	2	2	1	2	2	26
Aug. 6–27	2	2	2	2	2	2	2	2	1	2	2	1	0	0	22
Season total	6	6	6	6	6	6	6	5	5	6	6	4	4	4	76
Total for 12 months	18	18	18	17	23	22	23	17	17	20	20	20	17	17	267

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[2] Olson, F. C. W., and John B. Morrill, Jr. 1955. Literature survey of the Tampa Bay area. Armed Serv. Tech. Info. Agency, AD 81621 (Pt. 1): 66 p.p.

[3] The rainfall and temperature data used in this section are climatological normals (1931–60) compiled by the U.S. Department of Commerce, Weather Bureau, and published in the 1964 Annual Summary of Climatological Data For Tampa, Fla.

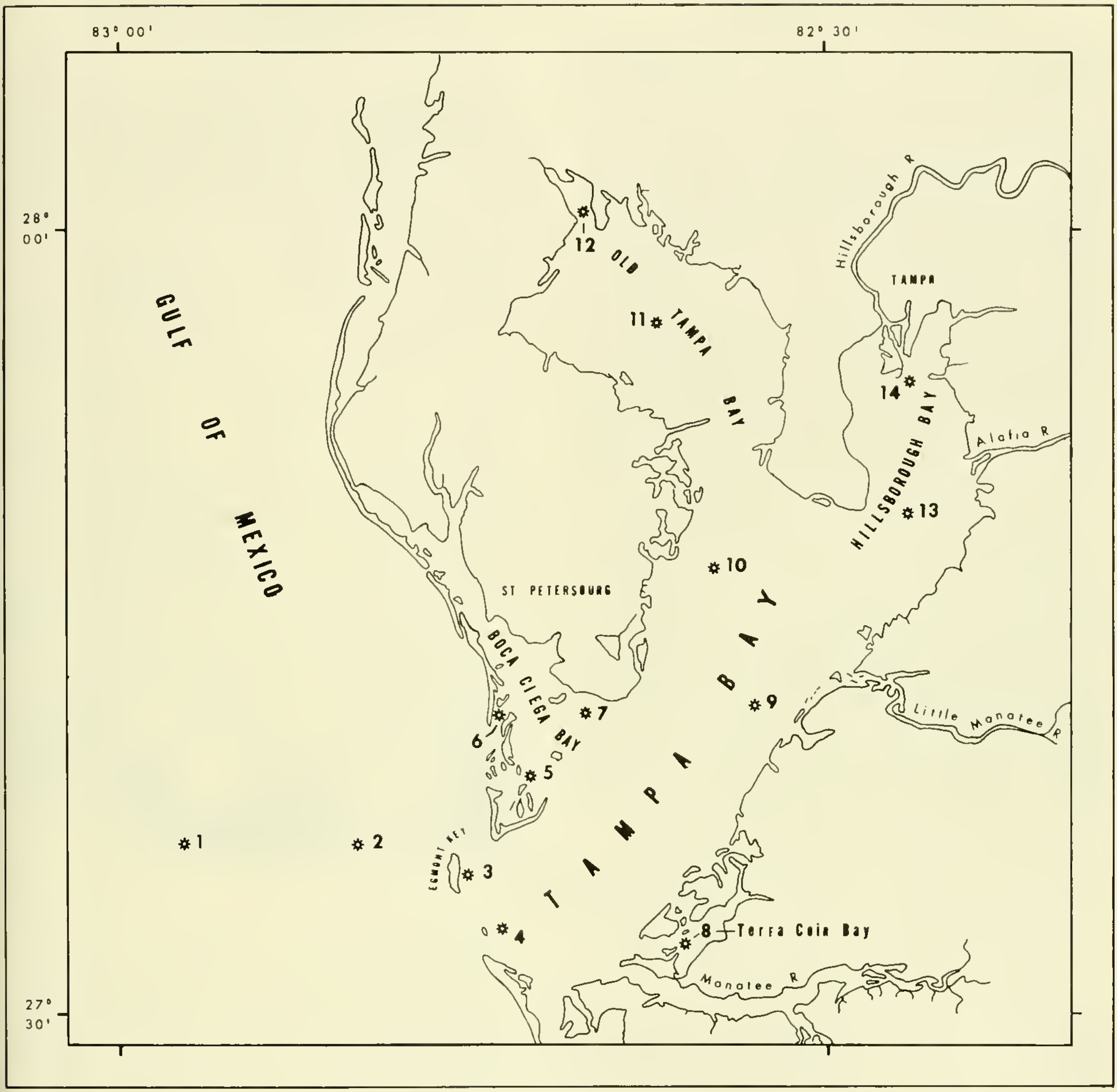
83° 00'
82° 30'
28° 00'
27° 30'
GULF OF MEXICO
OLD TAMPA BAY
TAMPA
Hillsborough R
HILLSBOROUGH BAY
Alafia R
ST PETERSBURG
BOCA CIEGA BAY
TAMPA BAY
Little Manatee R
EGMONT KEY
Terra Ceia Bay
Manatee R
1
2
3
4
5
6
7
8
9
10
11
12
13
14

FIGURE 1.—Sampling locations in Tampa Bay and the adjacent Gulf of Mexico.

nearly constant by maintaining a fixed engine speed. The volume of the cylinder of water strained through the net was determined to be 35 m.^{3} (calculated from the towing distance and the area of the net mouth). Since no correction was made to adjust for the effects of currents and clogging on the flow of water through the net, the quantitative data are not exact.

Plankton samples were preserved immediately after their collection in 5 percent neutralized formalin and stored in 30-oz. jars.

Water temperature and water sample (for salinity titration) were taken at the beginning of each plankton tow. Temperature was read to the nearest 0.1° C. with a thermister (Whitney[4] underwater thermometer, Model TC-5).

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[4] References to trade names in this publication do not imply endorsement of commercial products.

LABORATORY PROCEDURES

Plankton samples were placed in enameled photographic trays. Seaweeds and jelly fishes were removed from the samples manually, and the remaining volume was determined in the laboratory by the displacement method described by Thrailkill (1957). Plankton counts were made from aliquots whenever the wet plankton volume of the sample exceeded 0.5 ml. After the sample had been diluted to a known volume, usually 500 ml., four 5-ml. aliquots were withdrawn with a calibrated pipette. They were then transferred into a quadripartitioned petri dish for examination and counting under a binocular dissecting microscope. Samples having a wet volume of 0.5 ml. or less were transferred directly to petri dishes for counting. All samples were examined routinely for unusual organisms that might have been excluded from the aliquots. The mean number of organisms per cubic meter of water was calculated for each taxonomic group.

Body lengths of chaetognaths and fish larvae were measured-chaetognaths from the anterior extermity of the head to the tip of the caudal segment, excluding the caudal fin (Owre, 1960), and fish larvae from the snout to the base of the hypural plate (standard length).

ENVIRONMENTAL FACTORS

HYDROLOGY

The minimum and maximum water temperatures observed were 12.8° and 32.0° C. The smallest range in temperature at individual stations occurred in Boca Ciega Bay (15.3° C.), and the greatest (18.4° C.) in Old Tampa Bay (table 3). Seasonally, the range in mean temperatures between stations located on a traverse from offshore to Hillsborough Bay (stations 1, 2, 3, 4, 9, 10, 13, 14) was greatest in the spring (3.9° C.) and lowest in the winter (1.0° C.). These ranges in the fall and summer were 1.7° and 1.2° C. respectively.

Salinity was determined by Mohr-Knudsen method (Knudsen, 1901). Lowest salinities were usually in the upper area of Hillsborough Bay and highest 18.5 km. (10 nautical miles) offshore (table 3). The seasonal differences in mean salinities between these two areas (stations 1 and 14) were 8.62 p.p.t. (fall), 6.75 p.p.t. (winter), 8.03 p.p.t. (spring), and 13.58 p.p.t. (summer). The range in salinity at individual stations decreased progressively from upper Hillsborough Bay seaward. The smallest range was 18.5 km. offshore and the greatest in upper Hillsborough Bay, where temporal changes in salinity generally followed the dis-

TABLE 3.—*Mean surface water temperature and salinity for Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Seasons	Temperature at stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.
Fall	24.9	24.7	24.5	26.2	24.5	24.2	23.9	25.6	25.5	24.7	24.6	23.5	24.8	25.4
Winter	17.7	17.2	17.4	17.5	17.9	18.0	18.2	18.3	17.7	17.2	17.3	18.7	17.2	18.2
Spring	21.2	21.7	22.4	22.0	21.0	19.8	20.9	23.2	22.7	23.4	23.9	21.7	24.1	25.1
Summer	29.3	30.2	30.0	30.3	30.3	30.4	29.7	30.6	30.2	29.7	30.2	30.0	30.4	30.5
12 months	24.0	24.2	24.3	24.6	23.4	23.2	23.2	24.8	24.7	24.0	24.3	22.9	24.1	24.8
Minimum	15.3	15.1	15.4	15.4	14.3	15.2	15.4	15.1	15.4	13.8	13.2	12.8	13.4	13.8
Maximum	30.9	31.2	31.4	31.4	31.9	31.4	30.7	31.5	31.6	30.6	31.6	31.2	31.2	32.0
12-month range	15.6	16.1	16.0	16.0	17.6	16.2	15.3	16.4	16.2	16.8	18.4	18.4	17.8	18.2

Seasons	Salinity at stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰
Fall	34.96	34.54	34.03	33.80	32.30	32.94	31.82	31.15	29.53	28.29	25.73	24.66	27.27	26.34
Winter	34.45	33.64	33.82	33.20	33.01	33.22	32.01	31.96	30.52	29.39	27.76	26.86	28.38	27.70
Spring	34.89	34.30	33.76	33.97	33.90	33.79	32.44	31.57	31.19	29.45	29.06	28.52	28.10	26.86
Summer	35.67	35.31	34.99	35.16	33.98	34.62	32.59	30.56	29.46	27.90	28.46	28.05	25.96	22.09
12 months	35.07	34.52	34.23	34.18	33.34	33.67	32.23	31.26	30.17	28.74	27.89	26.96	27.46	25.81
Minimum	33.96	33.04	32.63	32.74	31.29	32.38	30.05	27.63	27.45	24.78	24.11	21.82	24.36	19.00
Maximum	35.93	36.00	35.58	36.00	35.35	35.39	34.33	33.68	33.13	30.79	29.83	29.67	29.85	28.51
12-month range	1.97	2.96	2.95	3.26	4.06	3.01	4.28	6.05	5.68	6.01	5.72	7.85	5.49	9.51

charges of the Hillsborough River [5]—the major source of river water to the bay (fig. 2).

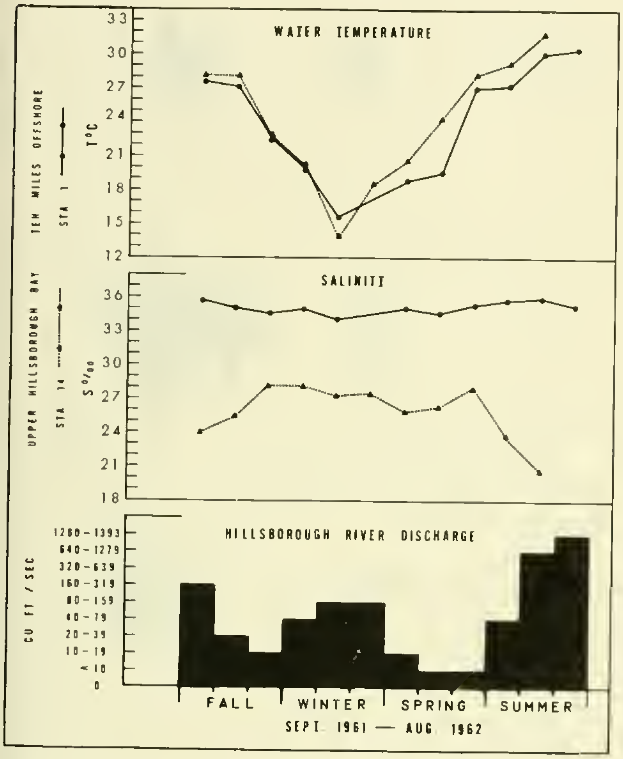

FIGURE 2.—Mean monthly discharge rate for the Hillsborough River and monthly surface water temperature and salinity for upper Hillsborough Bay (station 14) and 10 nautical miles offshore (station 1), September 1961 through August 1962. Mean values for temperature and salinity are given when two measurements of these variables were made in a month.

CLIMATOLOGY

Climatological data were taken from the records of the U.S. Weather Bureau for Tampa, Fla.

Rainfall was abnormally low during the study. From September 1961 through August 1962 total rainfall at Tampa, Fla., was 95.3 cm., 35.7 cm. below the climatological normal. Half of this amount (47.7 cm.) fell during the summer.

Mean monthly air temperatures at Tampa from September 1961 through August 1962 varied from 15.8° C. in January to 28.3° C. in July. Seasonally, mean air temperatures were 23.3° C. (fall), 16.7° C. (winter), 21.9° C. (spring), and 27.4° C. (summer).

ZOOPLANKTON VOLUMES

In 267 plankton tows, the volume of zooplankton per tow ranged from < 0.5 (considered as 0.25 ml. in all statistical treatments) to 92.0 ml. and averaged 7.0 ml. per sample. The greatest concentrations of macrozooplankton were in upper Tampa Bay, central Tampa Bay, lower Hillsborough Bay, central Old Tampa Bay, and 6.5 km. 3-½ nautical miles) offshore (fig. 3.

The abundance and composition of zooplankton varied widely by season and location. Twenty-five percent of the total volume was collected in the fall, 5 percent in the winter, 18 percent in the spring, and 52 percent in the summer (values adjusted for different numbers of tows per season). Coefficients of variation in zooplankton volume were calculated for each station to compare the areal variability of volumes (table 4). These coefficients

TABLE 4.—*Mean zooplankton volumes and the coefficients of variation of individual zooplankton volumes taken in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Seasons	Stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	ml.	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*
Fall	3.1	10.4	9.1	1.3	2.2	1.7	5.2	4.8	12.8	28.5	3.8	0.4	5.2	6.9
Winter	0.7	10.1	2.4	1.2	0.7	0.6	0.8	2.4	1.3	0.6	0.2	0.3	0.2	0.3
Spring	1.1	3.8	2.4	4.8	3.8	1.1	7.1	2.6	14.3	31.2	6.7	0.9	29.1	3.5
Summer	4.5	7.4	7.8	6.0	2.4	1.6	4.0	3.0	20.9	46.4	24.8	0.5	11.8	1.1
12 months	2.6	8.3	5.6	3.3	2.3	1.2	4.2	3.2	13.6	27.6	9.9	0.5	12.6	3.0
Minimum	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5
Maximum	20.0	35.0	26.0	21.5	10.0	5.0	24.0	12.0	62.0	86.0	50.0	3.0	92.0	25.0
Coefficient of variation	170	120	130	140	110	140	140	100	120	100	150	140	170	190

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[5] River discharge data (fig. 2) and rainfall data used in this section were taken from the 1961 and 1962 Surface Water Records of Florida, Vol. 1: Streams, compiled by the U.S. Department of the Interior, Geological Survey, and from the 1961 and 1962 Annual Summaries of Local Climatological Data for Tampa, Florida, published by the U.S. Department of Commerce, Weather Bureau.

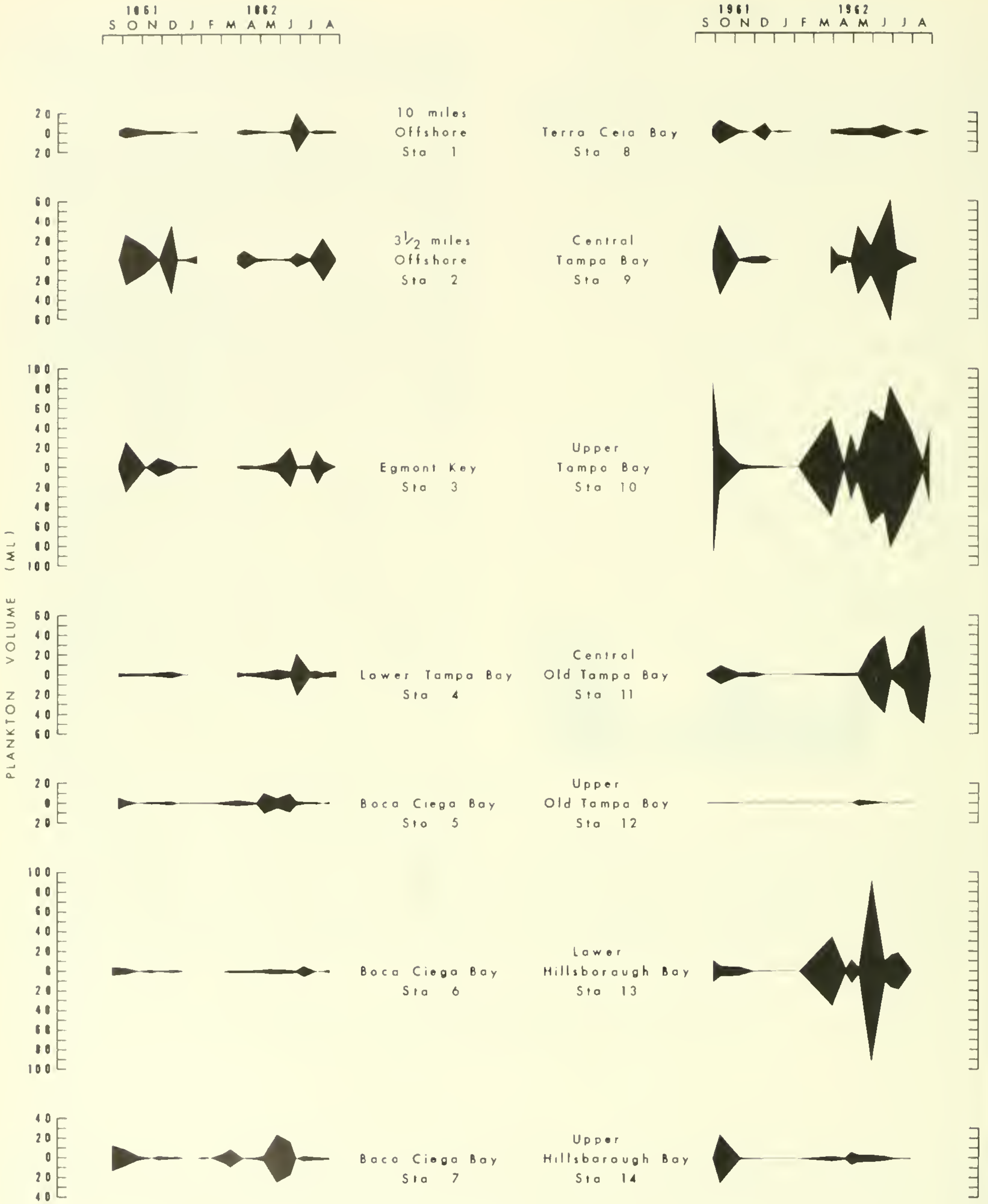

FIGURE 3.—Monthly plankton volumes for the surface waters of Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962. Plankton volume is expressed as milliliters per 35 m.³ of sea water.

varied from 100 to 190 percent. Greatest variations were at Hillsborough Bay and 18.5 km. offshore; minimum variations were in Terra Ceia Bay and in upper Tampa Bay.

CONSTITUENTS OF ZOOPLANKTON

The zooplankton consisted of holoplankton (53.5 percent), meroplankton (46.2 percent), and hypoplankton (0.3 percent). Most (87 percent) of the zooplankters in these categories were decapod crustaceans. Sixteen species, 24 genera, 30 families, and 21 taxonomic divisions higher than family were identified.

On the basis of abundance and frequency of occurrence the plankton is treated in three groups: major plankton; less abundant but frequently occurring and widely distributed organisms; and forms caught rarely.

MAJOR PLANKTON

Lucifer faxoni, larval porcellanids, and larval brachyurans, each of which accounted for 10 percent or more of the total number of organisms, were classified as major plankters. Collectively these taxa represented 83.5 percent of the zooplankton.

L. faxoni constituted 45.6 percent of the total number of zooplankters (table 5). It was the dominant zooplankter in Tampa Bay and was the only sergestid found. Most of the specimens were in the mastigopus phase, although protozoea and acanthosoma types were seen. It was collected at all stations and taken in numbers up to 1,051 per m.^{3}; 52 percent of *L. faxoni* were collected from the upper and central areas of Tampa Bay. This species was the most numerous organism in the fall, winter, and summer (fig. 4). As a result of its large size and numbers, *L. faxoni* accounted for 18.5 percent of plankton biomass. The monthly peaks in its displacement volume corresponded generally with the monthly peaks in the total volume of plankton.

Porcellanid larvae (zoea and megalops stages) formed the second most abundant group of organisms. They accounted for 27.4 percent of the total number of zooplankters and were collected in numbers up to 2,634 per m.^{3} They were most numerous in upper Tampa Bay and lower Hillsborough Bay and during the spring were the dominant organism in the area of investigation.

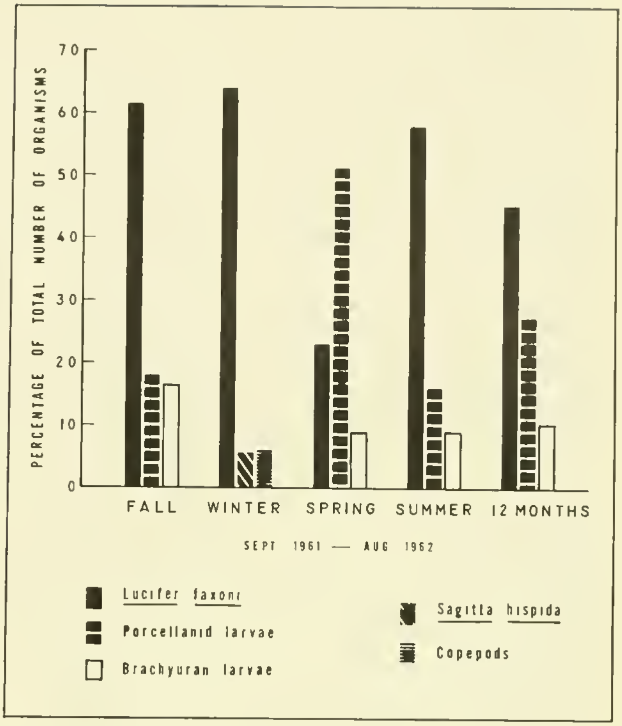

FIGURE 4.—Zooplankton taxa from Tampa Bay and the adjacent Gulf of Mexico that accounted for 5 percent or more of the organisms found during the periods shown, September 1961 through August 1962.

Except for Dromiidae, larval brachyurans were not identified to family and were classed only as zoea or megalops. Collectively they constituted 10.5 percent of the total number of zooplankters, and were the third-most-abundant taxon. Zoea and megalops were collected in numbers up to 251 per m.^{3} and 51 m.^{3} respectively. They were found at every station but appeared most abundantly in upper Tampa Bay and least abundantly in upper Old Tampa Bay. During the winter, megalops were absent at all stations in the upper portion of the area (stations 9 through 14).

In another and concurrent study, Dragovich and Kelly (1964) noted 2 species of adult Porcellanidae (*Petrolisthes galathinus* and *P. armatus*), 23 species of adult brachyurans (many of which were gravid), and a large number of juvenile portunids. Of the com-

TABLE 5.—*Frequency of occurrence and abundance (number per cubic meter in parentheses) of major zooplankters accounting for 10 percent or more of the total number of organisms collected in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Taxon and seasons	Frequency of occurrence and abundance per cubic meter (in parentheses)[1]								
	Stations								
	1	2	3	4	5	6	7	8	9
Lucifer faxoni:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Fall	4 (1.4)	4 (107.8)	4 (56.5)	2 (3.7)	5 (21.0)	4 (15.6)	4 (50.9)	4 (29.2)	4 (343.0)
Winter	3 (1.1)	4 (145.1)	4 (14.8)	3 (11.5)	5 (1.8)	6 (2.1)	6 (7.8)	4 (24.2)	3 (44.5)
Spring	4 (4.4)	4 (55.6)	4 (17.2)	4 (14.8)	6 (16.7)	4 (1.5)	5 (61.8)	4 (15.2)	5 (97.6)
Summer	6 (2.4)	5 (75.2)	6 (23.7)	6 (39.7)	6 (51.7)	6 (19.2)	6 (75.8)	5 (10.0)	5 (273.4)
12 months	17 (2.3)	17 (93.6)	18 (27.6)	15 (20.8)	22 (22.9)	20 (9.8)	21 (49.0)	17 (19.1)	17 (197.7)
Porcellanidae:									
Fall	4 (1.4)	4 (81.4)	3 (6.0)	3 (0.8)	3 (5.5)	3 (0.5)	4 (4.6)	4 (3.5)	4 (8.8)
Winter	1 (0.1)	3 (4.1)	4 (1.2)	2 (0.8)	5 (0.9)	6 (1.3)	4 (0.4)	3 (1.2)	1 (0.2)
Spring	4 (1.2)	4 (6.4)	4 (24.2)	4 (3.8)	6 (21.4)	3 (14.4)	5 (17.9)	4 (30.2)	5 (85.0)
Summer	4 (0.3)	5 (5.9)	6 (72.5)	6 (4.2)	6 (4.9)	5 (3.4)	5 (3.8)	5 (25.4)	4 (6.0)
12 months	13 (0.7)	16 (22.4)	17 (31.2)	15 (2.7)	20 (9.1)	17 (4.7)	18 (6.8)	16 (15.7)	14 (28.8)
Brachyura:									
Fall	4 (2.1)	4 (34.6)	4 (3.9)	3 (1.7)	5 (23.8)	4 (5.7)	5 (38.2)	4 (39.9)	4 (17.0)
Winter	3 (0.4)	3 (3.1)	4 (1.2)	2 (1.9)	3 (0.6)	5 (0.8)	4 (1.0)	4 (1.1)	1 (0.3)
Spring	4 (3.0)	3 (8.2)	4 (8.2)	4 (7.2)	6 (5.1)	2 (1.8)	5 (8.2)	4 (30.1)	5 (35.0)
Summer	6 (3.3)	6 (19.9)	6 (19.5)	6 (8.8)	6 (4.2)	6 (15.9)	6 (7.5)	5 (6.8)	5 (11.2)
12 months	17 (2.3)	16 (16.9)	18 (9.5)	15 (6.1)	20 (7.8)	17 (6.2)	20 (12 6)	17 (18.7)	15 (17.6)

Taxon and seasons	Frequency of occurrence and abundance per cubic meter (in parentheses)[1]						Percentage of total number of organisms collected	Maximum abundance
	Stations					All stations		
	10	11	12	13	14			
Lucifer faxoni:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*^{3}
Fall	4 (315.2)	4 (38.6)	2 (0.3)	4 (40.5)	4 (138.6)	53 (80.2)	61.6	1051
Winter	2 (4.8)	3 (1.0)	0 (0)	3 (0.8)	2 (1.1)	48 (15.8)	64.3	566
Spring	5 (167.4)	5 (11.3)	1 (0.2)	5 (174.6)	4 (7.0)	60 (47.7)	23.2	788
Summer	6 (492.5)	6 (107.3)	3 (0.4)	3 (97.2)	3 (8.0)	72 (91.3)	58.1	826
12 months	17 (253.8)	18 (43.0)	6 (0.2)	15 (83.9)	13 (36.8)	233 (60.4)	45.6	
Porcellanidae								
Fall	4 (9.6)	1 (0.1)	1 (0.1)	4 (3.9)	4 (7.9)	46 (9.2)	7.1	283
Winter	2 (0.3)	3 (0.3)	0 (0)	3 (0.4)	2 (0.4)	39 (0.8)	3.3	14
Spring	5 (386.0)	5 (8.2)	4 (1.1)	4 (774.6)	5 (41.6)	62 (105.8)	51.5	2634
Summer	6 (128.5)	5 (7.7)	4 (0.8)	4 (104 2)	4 (11.6)	69 (26.6)	16.3	471
12 months	17 (137.0)	14 (4.4)	9 (0.4)	15 (253.4)	15 (18.5)	216 (36.4)	27.4	
Brachyura								
Fall	4 (65.4)	3 (26.2)	1 (0.2)	4 (17.9)	4 (23.4)	53 (21.6)	16.6	202
Winter	3 (0.4)	3 (0.3)	0 (0)	2 (0.4)	3 (0.4)	40 (0.8)	3.3	11
Spring	5 (109.8)	5 (18.1)	2 (4.7)	5 (17.1)	4 (1.6)	58 (18.6)	9.1	236
Summer	6 (61.3)	6 (28.1)	3 (2.0)	2 (4.5)	3 (3.5)	72 (15.0)	9.2	262
12 months	18 (59.0)	17 (18.3)	6 (1.6)	14 (10.5)	13 (6.9)	223 (13.9)	10.5	

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[1] See table 1 for number of samples collected.

mercially important species they caught *Callinectes sapidus* and *Menippe mercenaria.*

LESS ABUNDANT BUT WIDELY DISTRIBUTED AND FREQUENTLY OCCURRING ORGANISMS

This group of organisms consisted of taxa that occurred in 10 percent or more of the samples (table 6). Collectively they accounted for 14 percent of the total number of zooplankters. Most taxa in this category appeared during every season.

Copepods were the fourth-most-numerous group collected. They occurred in highest numbers in the spring, and were the third-most-abundant taxon in the winter (fig. 4). Because of the coarse mesh of the plankton net, only larger specimens were retained consistently. Some of the nauplius and copepodite stages and smaller adults were held in the net only when trapped among larger plankton and detritus. *Labidocera aestiva* appeared to be the dominant form. The caligoids formed only a small part (1.8 percent) of this group.

Caridean shrimp constituted 2.4 percent of the zooplankters. Most of the specimens were advanced postlarvae and were classified only to family. Identified palaemonids were represented by the subfamilies Palaemoninae and Pontiniinae and the genera *Palaemonetes* and *Periclimines;* alpheids were represented by *Alpheus* and *Synalpheus* and hippolytides by *Tozeuma, Hippolysmata,* and *Latreutes fucorum. Tozeuma* ssp., found in stages from mysis to adult, accounted for 64 percent of the hippolytides. *Hippolysmata* sp. appeared only as advanced postlarvae and *Latreutes fucorum* only as adults.

Thalassinids were mostly advanced postlarval stages. Larvae of *Upogebia* sp. and *Callianassa* sp. also appeared in the samples. Some of these larvae possibly were *Upogebia affinis* and *Callianassa atlantica,* for both species are found in Tampa Bay.

Larval stomatopods were collected at every station during the summer. Antizoea, pseudozoea, erichtus, and alima types were in most of the samples. Possibly many of the larvae were *Squilla empusa,* a prominent organism in Tampa Bay (Dragovich and Kelly, 1964).

Twelve percent of the amphipods belonged to the suborder Caprellidea; the remainder belonged to one of the suborders, Gammaridea or Hyperiidea.

TABLE 6.—*Frequency of occurrence of zooplankters found in 10 percent or more of the samples from Tampa Bay and the adjacent Gulf of Mexico (excluding the three most abundant forms shown in Table 5), September 1961 through August 1962*

[Number of tows shown in parentheses]

Taxon	Frequency of occurrence [1]																				Percentage of total number of organisms collected	Maximum abundance
	During 12 months	Season [1]				Stations																
		F	W	S	S	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
	(267)	(59)	(65)	(67)	(76)	(18)	(18)	(18)	(17)	(23)	(22)	(23)	(17)	(17)	(20)	(20)	(20)	(17)	(17)		
Annelida:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*³
Terebellidae	47	6	4	12	25	0	3	8	8	9	4	0	1	0	4	6	0	4	0	1.8	128.0
Spionidae	42	9	11	8	14	1	3	4	2	3	2	0	11	0	4	7	1	4	0	0.4	46.0
Arthropoda:																					
Copepoda	177	38	42	45	52	2	15	17	15	16	12	9	15	13	19	16	4	14	10	2.7	188.0
Palaemonidae	158	35	30	52	41	13	4	12	11	20	13	13	17	8	11	14	8	11	3	1.3	37.0
Alpheidae	116	31	13	36	36	16	8	12	8	6	5	11	13	5	11	8	5	5	3	0.6	11.0
Stomatopoda	89	12	9	36	32	6	8	15	7	4	2	5	6	6	13	7	1	2	7	0.4	37.0
Hippolytidae	85	21	10	25	29	2	2	7	8	14	6	8	11	4	9	7	2	3	2	0.5	23.0
Thalassinidea	79	19	12	24	24	8	5	1	5	9	5	2	14	1	7	13	3	5	1	0.8	28.0
Amphipoda	48	7	17	15	9	0	1	3	4	12	6	1	6	2	5	4	3	1	0	0.1	3.0
Isopoda	35	7	13	7	8	2	0	0	0	2	2	2	6	0	1	1	13	2	4	<0.1	1.0
Penaeidae	26	4	1	1	20	5	4	1	2	2	5	1	1	0	2	1	1	1	0	0.2	34.0
Chaetognatha:																					
Sagitto hispida	133	24	31	38	40	9	12	16	15	10	8	10	13	7	11	9	6	3	4	1.2	34.0
Sagitto spp.[2]	107	19	11	34	43	6	11	8	12	11	7	8	9	8	10	6	4	5	2	1.2	97.0
Chordata:																					
Fish eggs	85	9	21	27	28	17	4	9	9	8	6	6	7	5	10	4	0	0	0	1.0	177.0
Appendiculariidae	83	18	13	27	25	4	9	10	11	10	4	0	14	3	4	7	0	7	0	1.3	37.0
Engraulidae	50	3	2	17	28	1	1	2	0	2	5	9	4	1	7	6	1	6	5	0.4	23.0
Sciaenidae	42	2	7	21	12	5	2	3	3	6	4	4	5	0	4	2	3	1	0	0.1	1.0
Clupeidae	39	3	15	19	2	3	5	2	0	8	8	5	2	1	2	0	2	1	0	0.1	3.0
Syngnatheidae	28	7	4	7	10	0	0	3	4	2	5	3	2	0	6	1	1	0	1	<0.1	0.5

[1] Fall, winter, spring, and summer.

[2] Immature *Sagitta* less than 5 mm long.

Most of the isopods were free-swimming cymothoids and were grouped in the genus *Aegathoa.*

Penaeids were represented by small numbers of larvae of *Sicyonia* spp., *Trachypeneus* spp., and *Penaeus duorarum; Sicyonia* (mainly mysis I and mysis III stages) constituted 36 percent of this family. They were restricted to the offshore area and lower areas of Tampa Bay (stations 1-4). Only two samples contained *Trachypeneus* larvae. The pink shrimp, *P. duorarum,* contributed 16 percent of the total penaeids. Postlarvae III stages of *P. duorarum* appeared most frequently; only occasional postlarvae I and II and mysis III were taken. These larvae were most abundant in the summer and were collected primarily in Boca Ciega Bay (station 6) and the immediately adjacent Gulf waters. Our observation of the temporal occurrence of larval stages of pink shrimp in Tampa Bay agrees generally with the findings of Eldred et al. (1965).

Appendicularia spp. and *Oikopleura* spp. were common appendiculariids and were found at most of the sampling locations.

A number of eggs and larval fish were collected. Many of the fishes were identified as commercially important species. The role of Tampa Bay in the production of species important in Gulf fisheries was discussed by Sykes and Finucane (1965).

Fish eggs were taken most frequently 18.5 km. offshore, but were most abundant at Egmont Key where 54 percent of the total number were collected. They were not identified.

Larval fish accounted for 0.8 percent of the total number of zooplankters. All engraulids were identified as *Anchoa* spp. Identified sciaenids were *Cynoscion* spp. and *Leiostomus xanthurus.* Larvae of *L. xanthurus,* 6 to 15 mm. long, were taken from late fall through early spring in Boca Ciega Bay and 6.5 km. offshore. *Cynoscion* spp. appeared infrequently during the spring and summer at most of the bay stations but were not found in Hillsborough Bay or offshore. Seventy-seven percent of the clupeids (3 to 20 mm. long) were identified as *Brevoortia.* All syngnathid larvae (5 to 44 mm. long) were of the genus *Syngnathus.*

Chaetognaths made up 3 percent of the total number of zooplankters. All undamaged specimens more than 5 mm. long were identified as *Sagitta. S. hispida* was the only chaetognath found throughout the area of investigation. It was plentiful in all seasons and was the second most abundant taxon during the winter (fig. 4). The broad dispersal and numerical abundance of immature *Sagitta* less than 5 mm. long suggest that *Sagitta* breed both in Tampa Bay and the adjacent offshore waters. The smallest chaetognath was 2.5 mm. long, but it is likely that smaller ones escaped through the net.

Polychaete larvae made up 2.4 percent of the total number of zooplankters. Terebellids (0.4 to 4 mm. long) were numerous in samples that contained a high proportion of *Bellerochea malleus.* The gut always contained large quantities of chlorophyll. None was identified to genus. Spionids (0.4 to 4 mm. long) were collected at 11 to the 14 sampling locations, but the genera *Polydora* and *Prionospio* were collected only off Egmont Key, in Boca Ciega Bay (station 6), and in Terra Ceia Bay.

FORMS RARELY CAUGHT

This group of organisms consisted of taxa which were in less than 10 percent of the samples (table 7). Only 10 of these taxa accounted for 0.1 percent or more of the total number of zooplankters, though many of them (e.g. pagurids, mollusks, and echinoderms) are common as adults of this area. The paucity of planktonic stages in this study may be ascribed partially to the large mesh of the collecting net and to the fact that only surface samples were taken.

The areal distribution of most of the plankters in this group was limited. Most of the cladocerans (66 percent), cirripedians (61 percent), and lancelets (60 percent) were collected in one sample taken during May from lower Hillsborough Bay. Fifty-three percent of the pagurids were taken in August in a single sample from upper Tampa Bay. Forty-two percent of the larval blennies were collected from the same area; they were present throughout the year but were most abundant in September. *Sagitta helenae* and *S. enflata* occurred fre-

TABLE 7.—*Frequency of occurrence of zooplankters found in less than 10 percent of the samples from Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

[Number of tows shown in parentheses]

Taxon	Frequency of occurrence [1]																				Percentage of total number of organisms collected	Maximum abundance
	During 12 months	Season [1]				Stations																
		F	W	S	S	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
	(267)	(59)	(65)	(67)	(76)	(18)	(18)	(18)	(17)	(23)	(22)	(23)	(17)	(17)	(20)	(20)	(20)	(17)	(17)		
Aschelminthes:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*³
Nematoda	2	-----	-----	2	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	1.0
Mollusca:																					
Gastropoda	17	5	9	1	2	-----	2	4	2	1	2	-----	4	-----	-----	1	1	-----	-----	<0.1	3.0
Pelecypoda	1	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	<0.1	0.5
Annelida:																					
Syllidae	9	1	3	2	3	-----	-----	3	-----	2	1	1	-----	-----	1	1	-----	-----	-----	<0.1	6.0
Nereidae	4	2	-----	-----	2	-----	1	-----	-----	1	-----	-----	-----	-----	1	1	-----	-----	-----	<0.1	3.0
Phyllodocidae	4	1	1	1	1	-----	-----	1	1	1	-----	-----	1	-----	-----	-----	-----	-----	-----	<0.1	1.0
Poecilochaetidae	3	-----	-----	3	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	<0.1	0.5
Sabellidae	2	-----	1	-----	1	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Polynoidae	1	-----	1	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Polychaetes (unidentified)	5	3	-----	1	1	1	-----	1	-----	1	-----	1	-----	-----	-----	1	-----	-----	-----	0.1	17.0
Arthropoda:																					
Paguridae	21	4	6	6	5	-----	-----	3	-----	-----	1	1	7	1	6	-----	1	-----	1	0.1	8.0
Cladocera	17	3	3	4	7	-----	3	6	2	1	-----	-----	2	-----	1	-----	-----	2	-----	0.8	217.0
Cirripedia	7	-----	2	4	1	-----	-----	1	1	1	-----	-----	1	-----	-----	-----	-----	3	-----	0.1	28.0
Cumacea	4	-----	2	-----	2	-----	1	-----	1	-----	-----	-----	1	-----	-----	1	-----	-----	-----	<0.1	3.0
Scyllaridea	4	2	-----	-----	2	1	-----	2	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	<0.1	0.5
Hippidae	3	2	-----	-----	1	1	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	8.0
Ostracoda	3	-----	2	-----	1	-----	-----	-----	-----	-----	-----	-----	2	-----	-----	1	-----	-----	-----	<0.1	0.5
Processidae	2	-----	1	1	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	6.0
Mysidacea	2	1	-----	1	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Euphausiacea	2	1	1	-----	-----	1	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Dromiacea	2	1	-----	-----	1	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Pycnogonida	1	-----	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Chaetognatha:																					
Sagitta helenae	24	3	5	6	10	17	4	1	1	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	0.2	30.0
Sagitta enflata	13	4	4	1	4	12	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.1	16.0
Sagitta tenuis	8	2	-----	2	4	6	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	1	-----	<0.1	2.0
Echinodermata:																					
Holothuroidea	1	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	<0.1	3.0
Ophiuroidea	1	-----	-----	-----	1	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Chordata:																					
Blenniidae	25	3	1	20	1	-----	-----	1	1	1	4	1	3	2	6	3	1	2	-----	0.1	7.0
Carangidae	15	3	-----	-----	12	-----	-----	2	1	1	2	1	-----	-----	4	4	-----	-----	-----	<0.1	0.5
Branchiostomidae	8	-----	1	4	3	-----	1	1	1	-----	-----	-----	4	-----	-----	-----	-----	1	-----	0.1	23.0
Thaliacea	8	3	1	2	2	6	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	3.0
Soleidae	8	1	-----	2	5	-----	-----	-----	-----	3	1	2	-----	-----	1	1	-----	-----	-----	<0.1	1.0
Triglidae	7	1	-----	3	3	-----	-----	2	-----	-----	2	-----	-----	-----	2	1	-----	-----	-----	<0.1	6.0
Gerridae	4	1	-----	-----	3	-----	-----	-----	1	-----	1	2	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Gobiidae	4	1	1	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	2	2	-----	-----	<0.1	0.5
Belonidae	2	-----	-----	-----	2	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Atherinidae	2	-----	-----	1	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	1	-----	-----	-----	<0.1	0.5
Cynoglossidae	1	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Fish larvae (unidentified)	38	4	8	10	16	5	2	3	4	1	-----	4	1	4	5	4	1	1	3	0.1	3.0

[1] Fall, winter, spring, and summer.

quently 18.5 km. offshore where they accounted respectively for 25 and 8 percent of the zooplankters collected in that area.

Forms identified in the samples but not included in the aliquots of samples that were counted were: the euphausiacean (*Euphausia americana*); cumacean (*Oxyurostilis* sp.); decapods (*Scyllarus* sp., *Emerita talpoida*, and *Dromidia antillensis*); lancelet (*Brachiostoma caribeum*); larval fish (*Strongilura timucu*, and *Prionotus* sp.); and polychaetes (*Nereis* sp., *Platynereis dumerilii*, and *Poecilochaetus johnsoni*). The present collection represents the first record of larval *P. johnsoni* from the southeastern United States (Taylor, 1966).

OCCURRENCE OF ZOOPLANKTON IN RELATION TO TEMPERATURE AND SALINITY

TEMPERATURE

To relate water temperature with the occurrence of the most plentiful zooplankton—22 taxa accounting for 98 percent of the total number of zooplankters collected — the temperature data were divided into three ranges (12.8° to 20.9° C., to 21.0° to 27.9° C., and 28.0° to 32.0° C.), each of which included about an equal number of temperature observations (table 8). Occurrences of plankton were adjusted for the differences in numbers of temperature observations in each range and ex-

TABLE 8.—*Percentage frequency of occurrence (adjusted for the difference in numbers of temperature and salinity observations in each range) of the most plentiful zooplankton at three salinity and temperature intervals, each of which includes about an equal number of observations—Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Taxon	Total occurrences	Temperature (° C.)[1]			Salinity (‰)[1]		
		12.8–20.9 (89)	21.0–27.9 (96)	28.0–32.0 (82)	19.0–29.4 (90)	29.5–33.4 (89)	33.5–36.0 (88)
	No.	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Annelida:							
Terebellidae	47	16.6	27.0	56.4	23.0	19.1	57.9
Spionidae	42	30.8	30.7	38.5	30.6	45.3	24.1
Arthropoda:							
Lucifer faxoni	233	29.6	34.6	35.8	27.6	36.4	36.0
Brachyura	223	28.1	33.6	38.3	28.8	34.0	37.2
Porcellanidae	216	30.5	32.5	37.0	31.6	31.9	36.5
Copepoda	177	33.2	30.2	36.6	33.0	32.7	34.3
Palaemonidae	158	31.6	33.3	35.1	30.0	36.7	33.3
Alpheidae	116	25.8	34.2	40.0	23.0	34.4	42.6
Stomatopoda	89	25.7	34.3	40.0	26.7	30.2	43.1
Hippolytidae	85	24.4	29.0	46.6	23.2	43.5	33.3
Thalassinidea	79	21.3	32.5	46.2	32.6	34.2	33.2
Amphipoda	48	39.8	35.1	25.1	22.6	43.7	33.7
Isopoda	35	31.7	43.0	25.3	62.6	25.9	11.5
Penaeidae	26	3.6	16.9	79.5	19.0	11.6	69.4
Chaetognatha:							
Sagitta hispida	133	32.8	29.1	38.1	20.0	39.0	41.0
Sagitta, spp.[2]	107	26.6	24.6	48.8	23.1	32.6	44.3
Chordata:							
Fish eggs	85	37.7	31.6	30.7	13.9	35.1	51.0
Appendiculariidae	83	31.2	31.1	37.7	20.2	36.0	43.8
Engraulidae	50	13.8	32.9	53.3	45.6	32.1	22.3
Sciaenidae	42	43.0	31.1	25.9	18.8	42.7	38.5
Clupeidae	39	60.6	36.6	2.8	10.0	53.8	36.2
Syngnatheidae	28	24.8	29.5	45.7	24.7	39.2	36.1

[1] Total number of temperature and salinity observations within each range shown in parentheses.

[2] Immature *Sagitta* less than 5 mm. long.

pressed as percentage frequency of occurrence. Seventeen of the taxa occurred most frequently at the highest range, one at the intermediate range, and four at the lowest range. These observations suggest that for most zooplankton low temperatures were more restrictive than high.

SALINITY

The study of the relation of salinity to the occurrence of zooplankton was similar to that for temperature. The salinity ranges used were 19.0 to 29.4 p.p.t., 29.5 to 33.4 p.p.t., and 33.5 to 36.0 p.p.t. (table 8). Eleven of the 22 taxa occurred most frequently at the highest range, nine at the intermediate range, and two at the lowest range. These comparisons suggest that low salinity restricts the distribution of zooplankton in Tampa Bay.

The zooplankton included both euryhaline and marine forms. *Lucifer faxoni*, porcellanids, copepods, and chateognaths were taken throughout the entire salinity range (19.0 to 36.0 p.p.t.). The range for *L. faxoni* was similar to the range (19.3 to 34.2 p.p.t.) given by Woodmansee (1958) in Biscayne Bay, Fla.

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THE GEOSTROPHIC CIRCULATION AND DISTRIBUTION OF WATER PROPERTIES OFF THE COASTS OF VANCOUVER ISLAND AND WASHINGTON, SPRING AND FALL 1963

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ABSTRACT

Analysis of oceanographic data collected during the spring and fall cruises of the RV *George B. Kelez* in 1963 within 220 kilometers of the coasts of Vancouver Island and Washington indicated a net volume transport toward the north; the flow was about 3 x 10^6m.^{3} sec. off northern Vancouver Island, but only 1 x 10^6m.^{3}/sec. off Washington.

The major structural features were consistent in each of the nine vertical sections of salinity, temperature, or dissolved oxygen normal to shore between the Columbia River and Cape Cook.

A water mass that had higher salinity, higher temperature, and lower dissolved-oxygen concentration than offshore water existed over the continental slope below the halocline. The implied northward flow at depth along the coast was very weak. These data add to the increasing body of information concerning the California Undercurrent.

At a conference on fishery-oceanography at San Francisco, Calif., on June 2, 1947, the need became obvious for repeated oceanographic surveys along the Pacific coast up to about 500 km. offshore (Sette, 1947). A gap existed at the time of this conference between proposed sampling off the California coast by Scripps Institution of Oceanography and off the Canadian coast by the Pacific Oceanographic Group. This gap narrowed when the Department of Oceanography, at Oregon State University, began a survey of Oregon coastal waters in June 1958, and the Department of Oceanography at the University of Washington in January 1961 began a study of the area influenced by the Columbia River effluent. Extensive oceanographic observations from the Columbia River to northern Vancouver Island in the spring and fall of 1963, by the Oceanographic Section of the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., also filled in a portion of the gap. The purpose of the spring cruise was to determine oceanographic conditions in the coastal environment within 185 km. of shore (Ingraham, 1964); the fall cruise was planned to determine whether significant changes had occurred since spring. The locations of oceanographic stations for both cruises are shown in figure 1.

This report presents the significant features of the distributions of salinity, temperature, dissolved oxygen, and water mass and the circulation as shown by geostrophic currents at the surface and at 200 meters.

CIRCULATION

Interesting aspects of the circulation close to the coast are the extent, continuity, and source of the surface Davidson Current and of the subsurface California Undercurrent, and the relationship of the two. The flow in the Davidson Current has been clearly shown by drift bottles released during fall, winter, and early spring from as far south as central California and recovered along the coast of British Columbia. This surface current extends at least 93 km. from shore; it usually has an average speed of about 15 cm./sec. but speeds of about 40 cm./sec. have been found (Schwartzlose, 1963). Burt and Wyatt (1964) reported similar minimal velocities for drift bottles released off Oregon during January 1961 and recovered off Vancouver Island.

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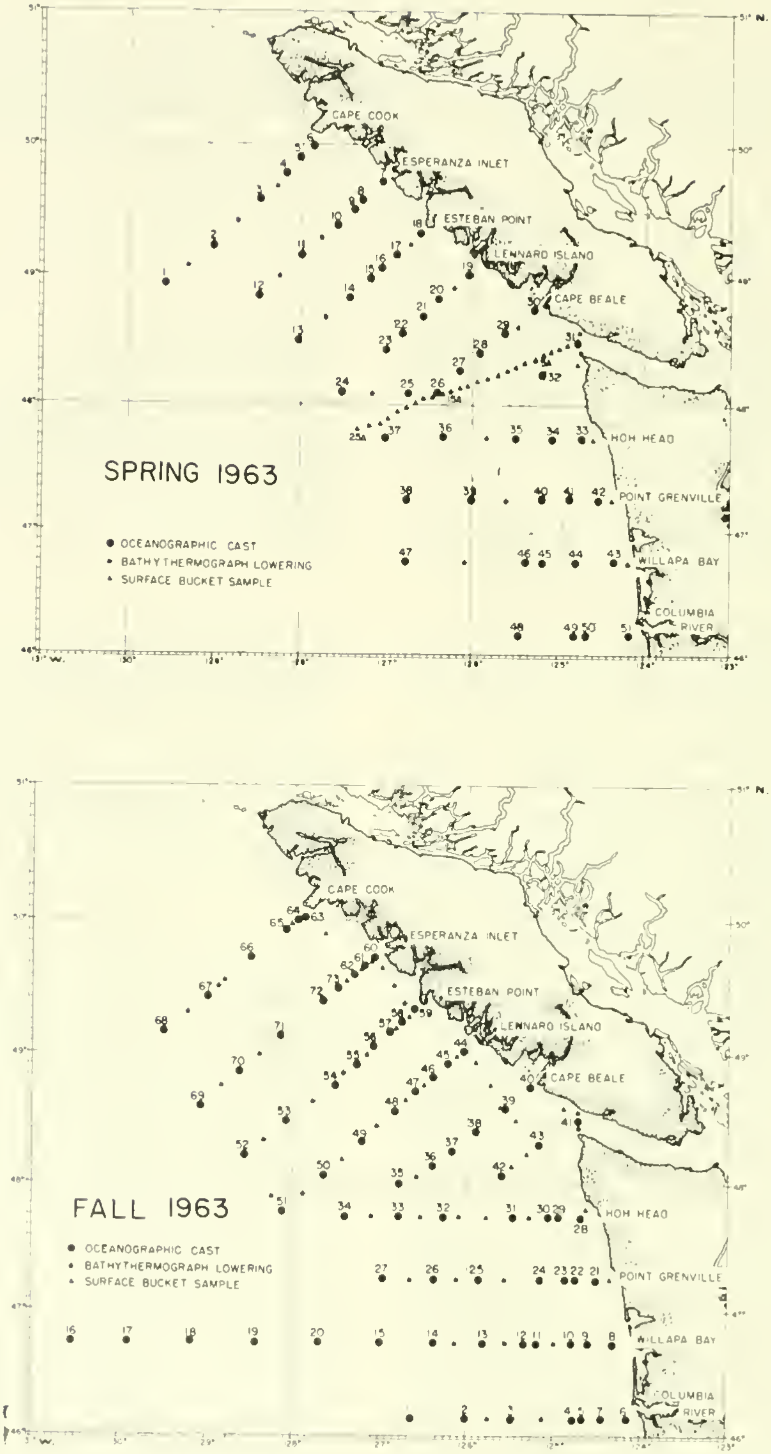

SPRING 1963
CAPE COOK
ESPERANZA INLET
ESTEBAN POINT
LENNARD ISLAND
CAPE BEALE
HOH HEAD
POINT GRENVILLE
WILLAPA BAY
COLUMBIA RIVER
● OCEANOGRAPHIC CAST
• BATHYTHERMOGRAPH LOWERING
▲ SURFACE BUCKET SAMPLE
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
FALL 1963
CAPE COOK
ESPERANZA INLET
ESTEBAN POINT
LENNARD ISLAND
CAPE BEALE
HOH HEAD
POINT GRENVILLE
WILLAPA BAY
COLUMBIA RIVER
● OCEANOGRAPHIC CAST
• BATHYTHERMOGRAPH LOWERING
▲ SURFACE BUCKET SAMPLE

FIGURE 1.—Locations of oceanographic stations, RV *George B. Kelez*, April 30, to May 17 and October 23 to November 24, 1963. (The 183- and 1,829-m. depth contours are shown.)

The cause of the Davidson Current is not clearly understood. Off the coast of Oregon it appears to result from local wind stress, but direct measurements during October 1958 and January 1959 (Reid and Schwartzlose, 1963) indicate that the driving force of this current is not local winds; it may be a surface manifestation of a deeper northward-flowing countercurrent that develops when winds weaken seasonally (Sverdrup, Johnson, and Fleming, 1942). This northward countercurrent which opposes the offshore California Current has been reported off central California below 200 m. throughout the year (Reid, Roden, and Wyllie, 1958). Northward flow also was reported off Washington and Oregon below 200 m. during the summers of 1955–57 and 1959; this report was based upon limited observations (Dodimead, Favorite, and Hirano, 1963). Our closely spaced observations during 1963 permit a more detailed evaluation of the size and continuity of the surface Davidson Current, the subsurface California Undercurrent, and other major features of the circulation off the coasts of British Columbia and Washington.

GEOSTROPHIC CURRENTS

Geostrophic currents reflect the general circulation associated with the distribution of mass. They are calculated from an arbitrarily selected reference depth and are, therefore, relative currents. The 1,000-db. (decibar) surface has been used as a reference surface in the North Pacific Ocean by Reid (1961), Dodimead et al. (1963), Budinger, Coachman, and Barnes (1964), and Favorite (1966) because they had

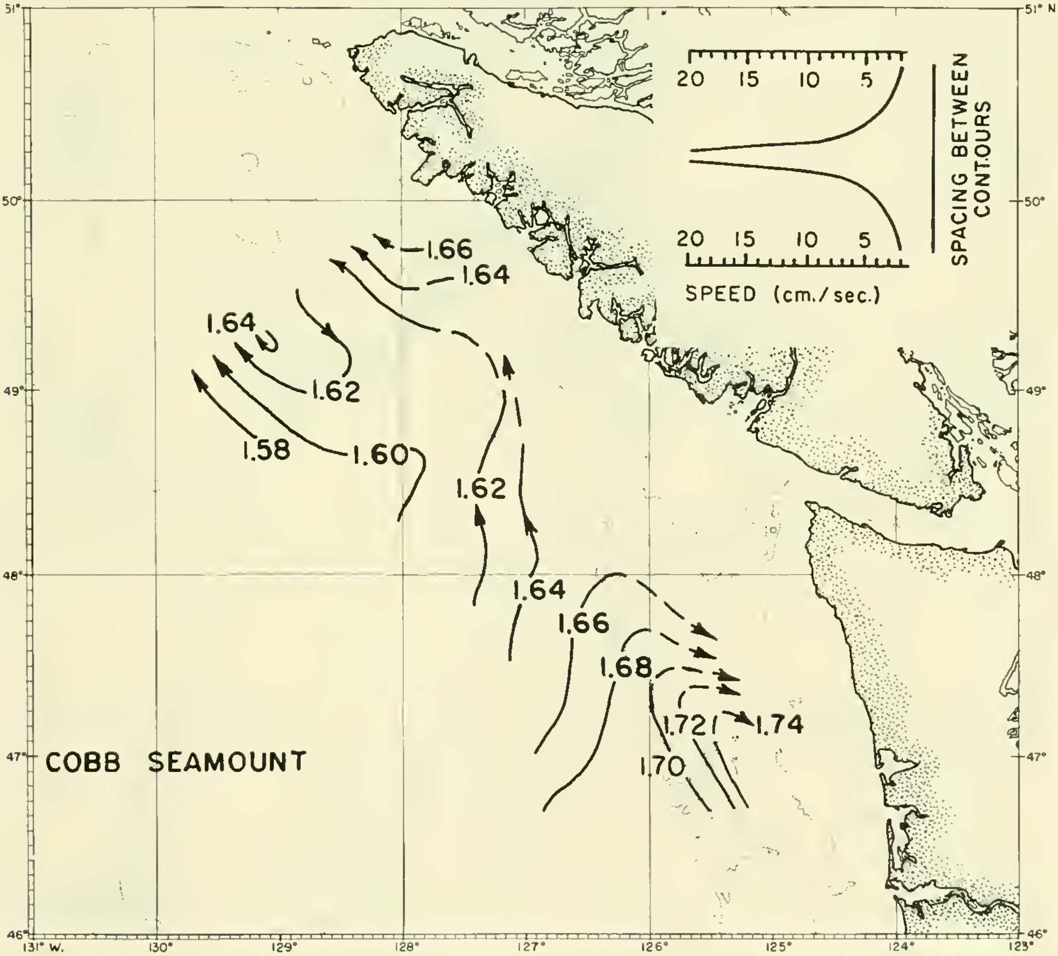


FIGURE 2.—Geopotential topography, 0/1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

sufficient data only to 1,000 m. Bennett (1959), using a deeper reference level, obtained greater surface velocities for the Gulf of Alaska. In the absence of a known depth of no motion, the deepest level compatible with all the data (1,500 db.) was selected for the reference surface in this study. Other assumptions that limit the accuracy of geostrophic currents are: (1) synoptic data, (2) unaccelerated flow, (3) lack of internal wave or tidal influence, and (4) absence of friction.

Caution must be used in the estimation of the surface velocity from geostrophic currents alone. The Ekman Current (Sverdrup et al., 1942) caused by local, variable wind stress must be added to the geostrophic current, for it is reasonable to assume in the absence of direct measurements of current that the Ekman velocities at the surface may exceed the surface geostrophic velocities. Examination of transport values computed from mean monthly pressure charts (Fofonoff and Ross, 1961) suggests that Ekman velocities of 3 to 10 cm./sec. generally toward the southeast may be expected in this coastal area during spring and fall. Although the short-term Ekman Currents, averaged on a daily basis, may be even greater, they are negligible below 200 m. They were neglected in this discussion which is concerned primarily with the main portion of the water column below 200 m.

The data from the cruises of the *Kelez* permit construction of the first geostrophic current charts off the Washington coast from a reference level of 1,500 db. Relative currents flow along contour lines of equal geopotential

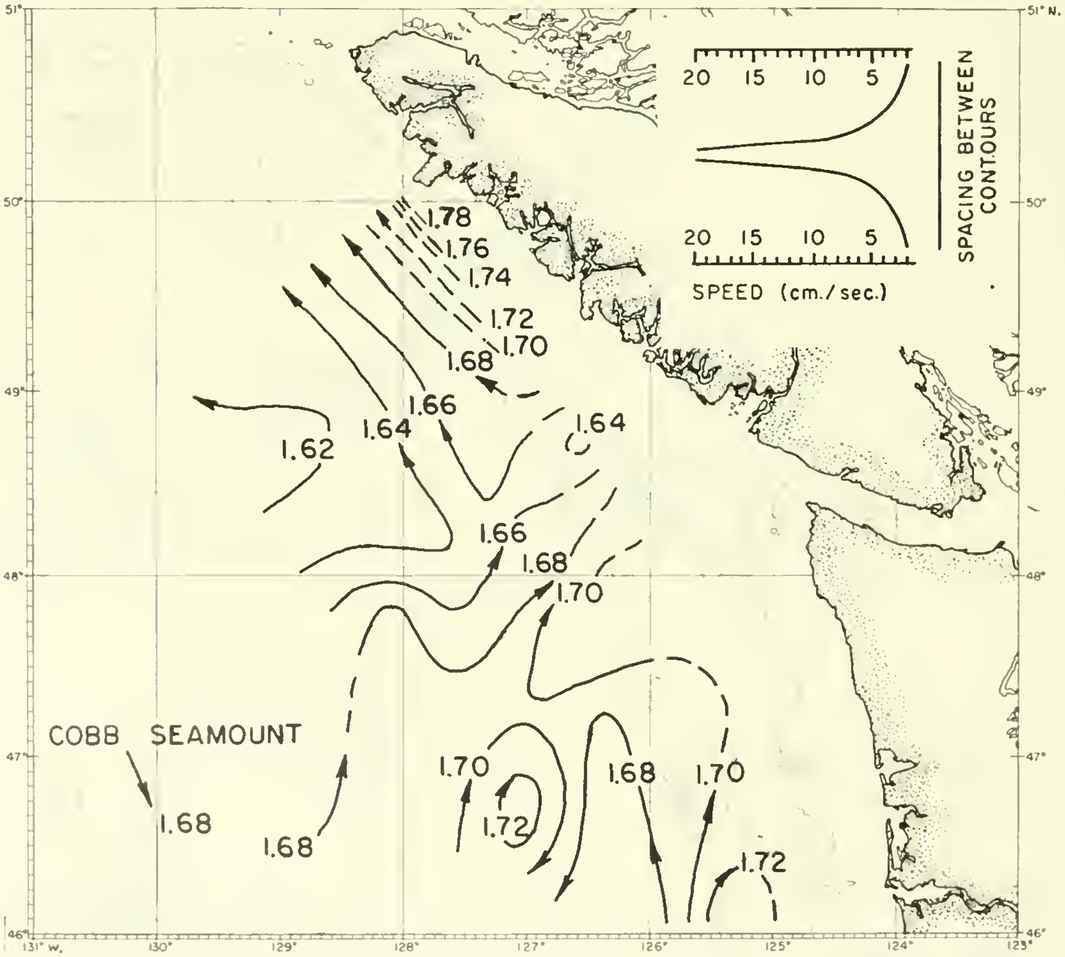

51°
51° N.
50°
50°
49°
49°
48°
48°
47°
47°
46°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
20 15 10 5
20 15 10 5
SPACING BETWEEN CONTOURS
SPEED (cm./sec.)
1.78
1.76
1.74
1.72
1.70
1.68
1.66
1.64
1.62
1.64
1.66
1.68
1.70
COBB SEAMOUNT
1.68
1.68
1.70
1.72
1.68
1.70
1.72

FIGURE 3.—Geopotential topography, 0/1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

depth with speed proportional to the gradient across them. Broken lines (figs. 2–5) represent currents in water shallower than the reference depths, which are calculated by the method used by Bennett (1959).

Surface Currents, 0 to 1,500 db.

Eddies complicated the pattern of surface geostrophic currents during the spring, but the predominant surface current within 185 km. of shore was generally toward the north (fig. 2). A major feature was the apparent divergence of onshore flow near southern Vancouver Island. North of the divergence, water from offshore veered toward the northwest and flowed generally parallel to the coast. Northwestward velocities were 10 and 12 cm./sec. at two locations on the northernmost line of stations, and a speed of 18 cm./sec. occurred off the Washington coast near lat. 47° N. The latter flow turned eastward toward shore and was not evident north of lat. 47°30′ N.

Although large eddies were also present off the coast of Washington during fall, they were absent off Vancouver Island (fig. 3). Maximum speed off the coast of Washington was 11 cm./sec. in the anticyclonic eddy near lat. 47° N., long. 127° W. The northward flow of 10 cm. sec. off the Columbia River in the vicinity of the 1,829-m. depth contour appeared to be dissipated by eddies as it proceeded north. Offshore water near lat. 48° N. flowed northeasterly toward southern Vancouver Island as it had during spring, but the distinct divergence over the continental slope was absent in the fall, and most of the water appeared to flow

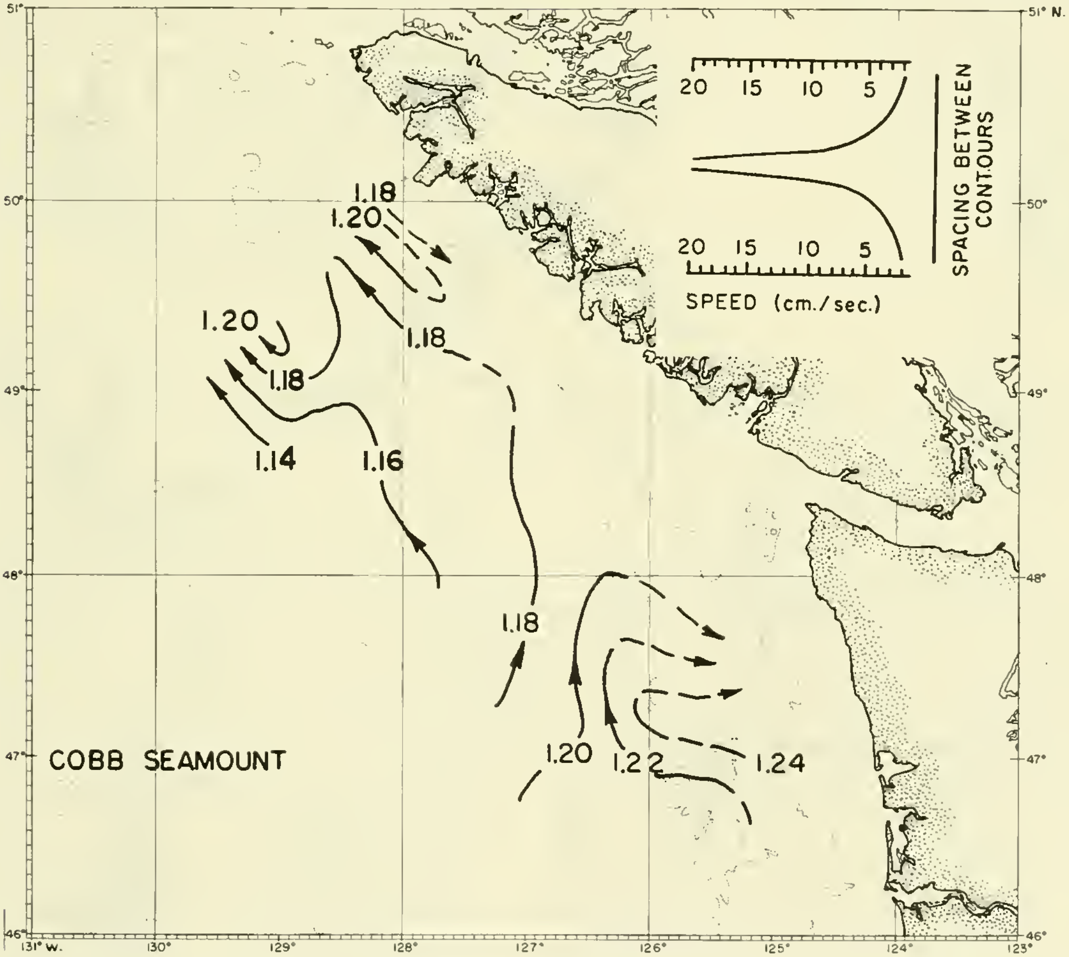


FIGURE 4.—Geopotential topography, 200/1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

northwesterly along the coast. A maximum speed of 20 cm./sec. occurred close to shore near Cape Cook.

Results from additional stations along the Willapa Bay line at 30-mile intervals to Cobb Seamount indicated that just east of Cobb Seamount was a weak southerly flow which suggests a meander in the general onshore movement.

In summary, the gross aspects of the surface geostrophic currents during spring and fall were similar. A major, recurring feature was the broad northeasterly movement of offshore water toward southern Vancouver Island; this flow veered northwesterly generally parallel to the coastline. Most characteristic features of the circulation off Washington were the many eddies and the apparent lack of strong northward flow of near-shore water, the Davidson Current, across lat. 48° N. Drift bottle experiments during the winter of 1965, however, indicated a significant northward flow of water over the Continental Shelf off Washington and Vancouver Island. The onshore flow which restricts the northward movement of water along the coast of Washington suggests a cause for the formation of eddies.

Lower Zone Currents, 200 to 1,500 db.

Data collected during the spring and fall of 1963 indicate the bottom of the halocline did not extend to a depth of 200 m. in the coastal area. Geostrophic currents at 200 m., therefore, represent the movement of water which possesses nearly constant properties below the halocline and is isolated from the direct in-

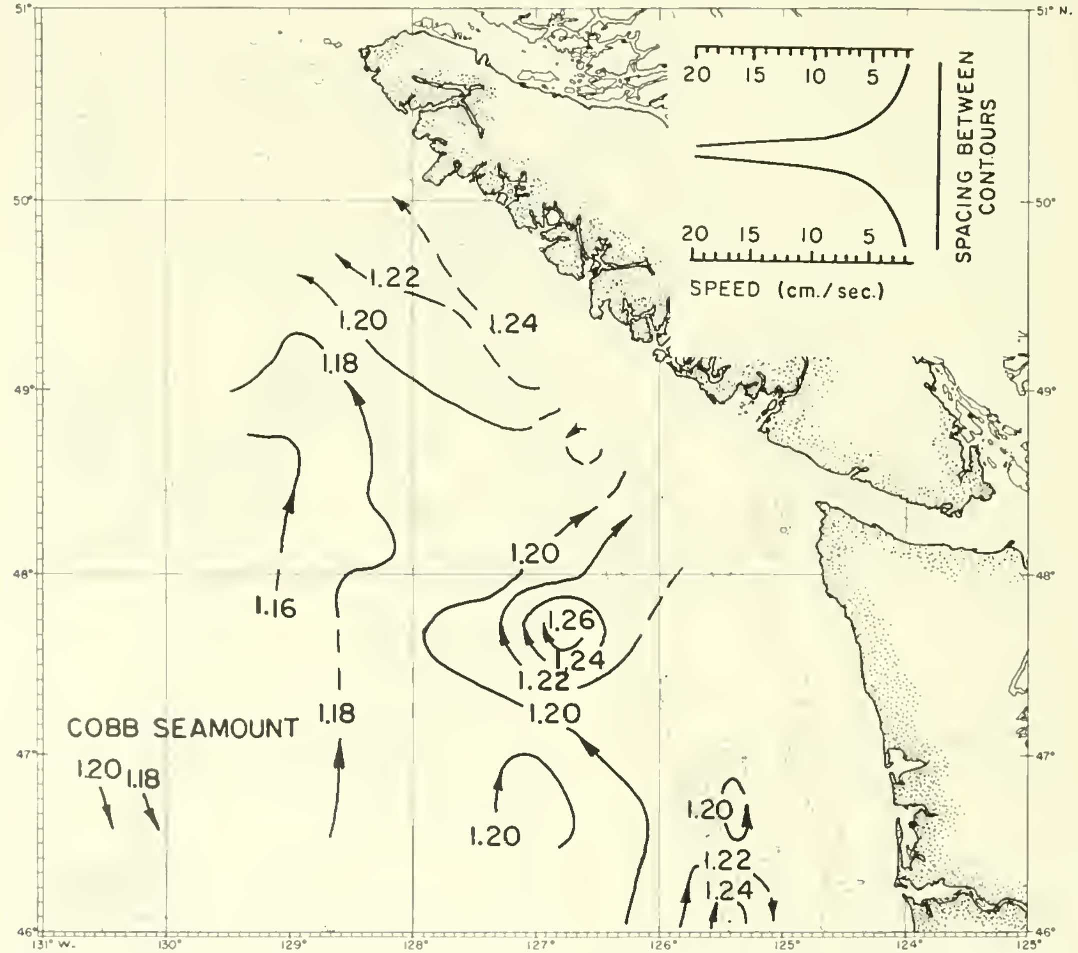

51°
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
20 15 10 5
20 15 10 5
SPEED (cm./sec.)
SPACING BETWEEN CONTOURS
1.22
1.24
1.20
1.18
1.16
1.20
1.26
1.24
1.22
1.20
1.18
COBB SEAMOUNT
1.20
1.18
1.20
1.20
1.22
1.24

Figure 5.—Geopotential topography, 200/1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

fluence of seasonal processes (Tully and Barber, 1960). During spring the directions of geostrophic flow at 200 m. and at the surface were nearly identical (fig. 4). An exception occurred near lat. 47° N., where water on the Continental Slope veered more sharply offshore than did the surface water. The deeper flow followed the 1,829-m. (1,000-fathom) depth contour and appeared to be influenced by the local bottom topography. The maximum current of 10 cm./sec. was at 200 m., whereas the surface flow was 6 cm./sec. This condition is contrary to the characteristic decrease in speed with depth throughout most of the Subarctic Region and occurred only in this one area off the coast of Washington.

Geostrophic currents at 200 m. during fall also followed closely the direction of the surface currents (fig. 5). The speed at 200 m. was generally one-half that of the surface current north of lat. 48° N., but speeds significantly greater than the surface flow were again present off Washington. The speed of the pronounced anticyclonic eddy just south of lat. 48° N. near the 1,829-m. depth contour was 15 cm./sec., at least three times the speed at the surface.

When Dodimead et al. (1963) showed the California Undercurrent flowing northward below 200 m., the surface water flowed south, opposing the Undercurrent. Because there was no southerly surface flow during the spring and fall of 1963, this apparent reversal did not exist; but if the surface current was the slower, the Undercurrent would be evident as a relative maximum at 200 m. in the velocity profile. The vertical distribution of velocity in the upper 1,500 m. during the fall, seaward from Willapa Bay, Hoh Head, and Esperanza Inlet, showed an area within 165 to 220 km. of the Washington coast in which pronounced maxima in the velocity did occur between depths of 200 m. and 300 m. (fig. 6). The direction of flow in adjacent maxima opposed each other, apparently forming eddies. The resultant current across any line normal to the coast of Washington, although northward, was very small. Volume transport calculations indicate the magnitude of the net flow.

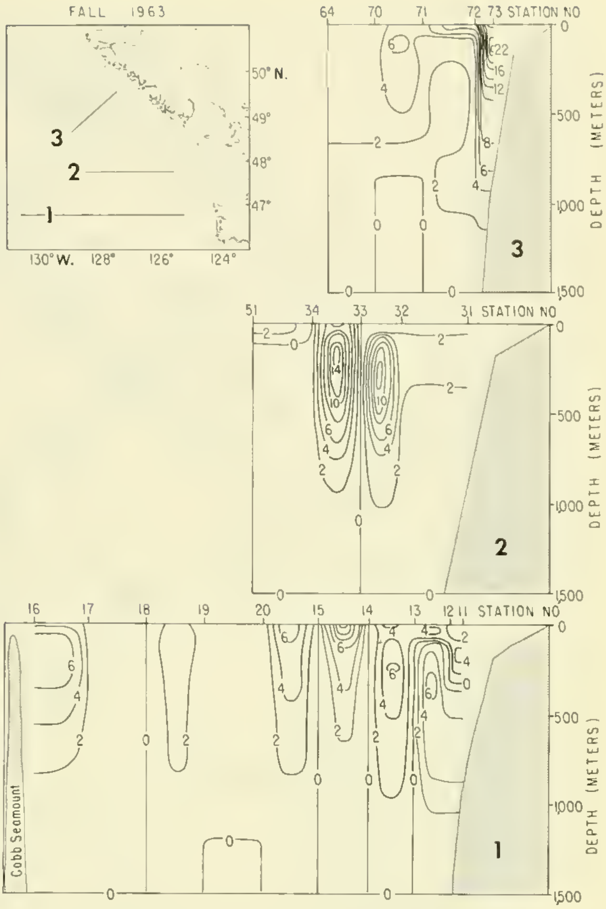


FIGURE 6.—Vertical sections of geostrophic velocity (cm./sec.) relative to 1,500 db. seaward from Willapa Bay, Hoh Head, and Esperanza Inlet, fall 1963. (Light shading indicates regions of northward flow.)

VOLUME TRANSPORT

Volume transports are calculated by integrating the geostrophic currents throughout the water column (Sverdrup et al., 1942). The volume transports indicate the resultant relative flow through the selected cross-sectional area, and are, therefore, a more reliable representation of the net flow in an area than a chart of the geostrophic currents at a particular depth. In the previous section on geostrophic currents, I pointed out that surface Ekman currents which were neglected may be in the same order of magnitude as the surface geostrophic velocities. In terms of the net transport in this coastal area during spring

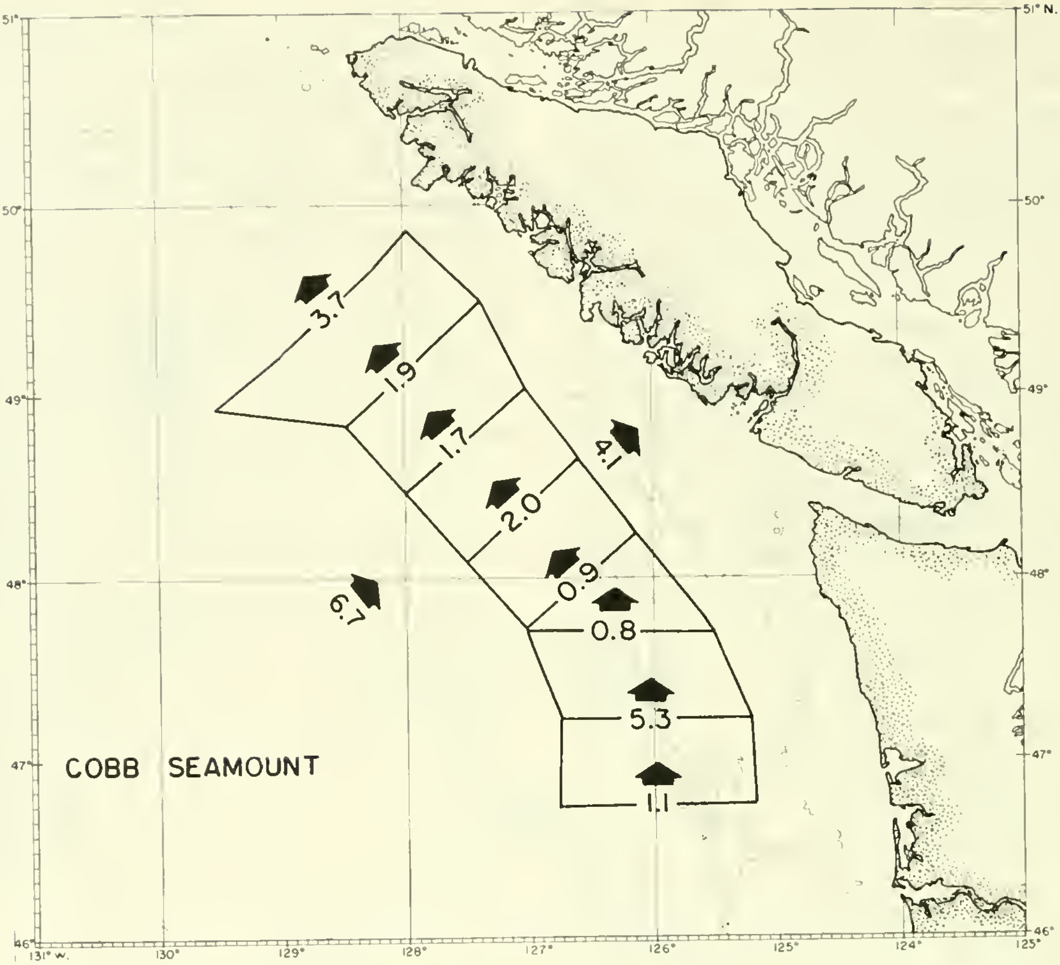


FIGURE 7.—Volume transport in 10^6m.^{3}/sec., 0 to 1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

and fall the zonal and meridional components of Ekman Transport computed by Fofonoff and Ross (1961) appear to contribute only 0.01 x 10^6m.^{3}/sec. and thus may be neglected.

During spring the net transport of water across each of the eight lines normal to the coast was directed toward the north and averaged approximately 2 x 10^6m.^{3}/sec. (fig. 7). This estimate appeared to give considerable credence to the existence of both the Davidson Current and California Undercurrent. On the other hand, the large northward flow of 5.3 x 10^6m.^{3}/sec. off the coast of Washington was part of an anticyclonic eddy; only a very weak net transport of less than 1 x 10^6m^3/sec continued northward across lat. 48° N. A relatively large volume 6.7 x 10^6m.^{3}/sec. entered the area from offshore, of which 4.1 x 10^6m.^{3}/sec. apparently flowed onshore across the Continental Slope where calculation of volume transport to 1,500 m. is less meaningful. The net northward transport increased to 3.7 x 10^6 m.^{3}/sec. across the northernmost line and had the same direction and magnitude as that reported by Bennett (1959) during August 1955 for the near-shore area between lat. 50° and 55° N., just north of this study area.

During fall the greatest northward transport again occurred off the northern coast of Vancouver Island; no significant change appeared in the volume of water flowing northward past Cape Cook (fig. 8). Off the Washington coast the net transport was again about 1 x 10^6m.^{3}/sec., but the direction reversed across succes-

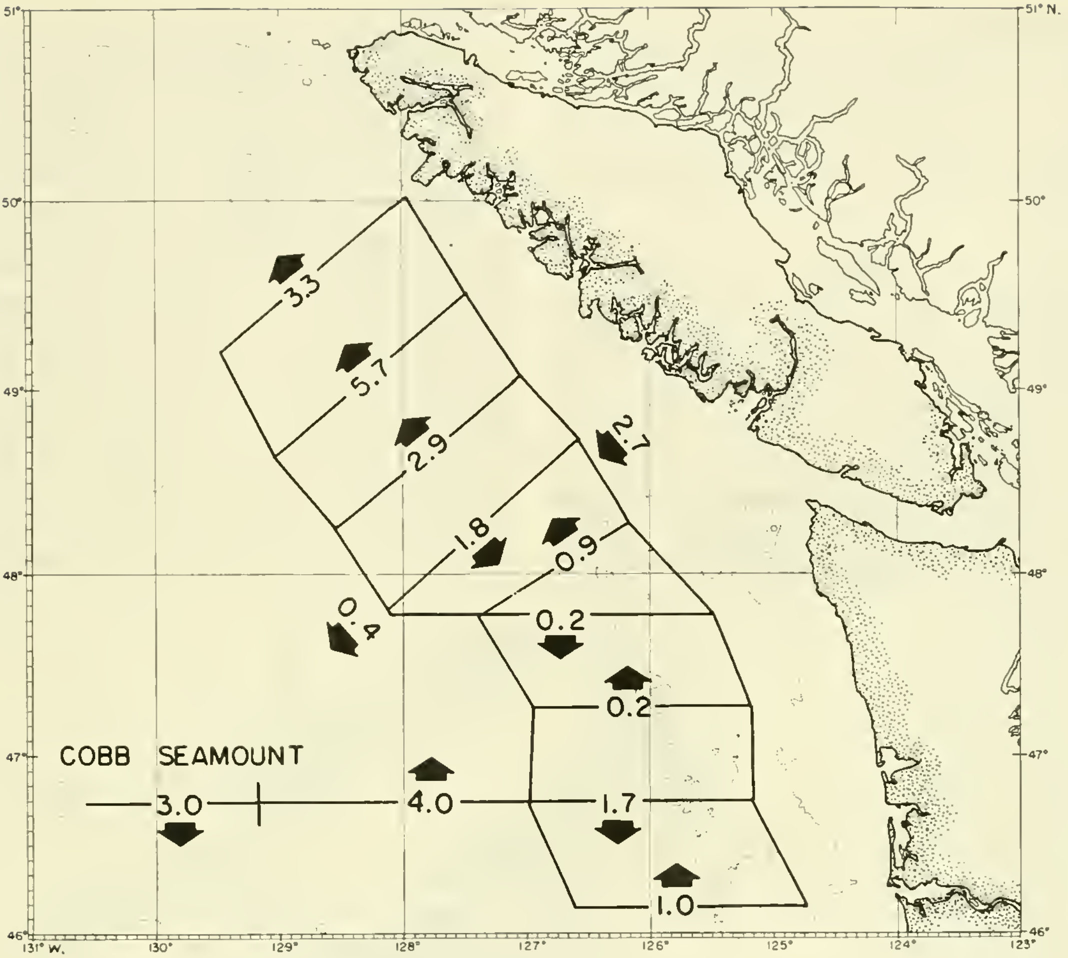


FIGURE 8.—Volume transport in 10^6m.^{3}/sec., 0 to 1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

sive lines normal to shore. The onshore movement evident during spring had reversed to 0.4 x 10^6m.^{3}/sec. in the offshore part of the area and 2.7 x 10^6m.^{3}/sec. Seaward across the Continental Slope. The net transport across the line from Willapa Bay to Cobb Seamount was less than 1 x 10^6m.^{3}/sec. Compared with a transport of 14 x 10^6m.^{3}/sec. for the Gulf of Alaska (Bennett, 1959), these results indicate a lack of significant net transport along the coast of Washington within 500 km. of shore.

The surface Davidson Current and the subsurface California Undercurrent reported by previous authors, therefore, did not contribute more than 1 x 10^6m.^{3}/sec. to the net northward transport of water along the coast of Washington. Although the total volume of transport was the same in spring and fall, an increase in the California Undercurrent was implied by the distribution of properties at and below 200 m. south of lat. 48° N.

DISTRIBUTION OF PROPERTIES

Although the most common method of determining oceanic circulation is the calculation of geostrophic currents and transports from observed values of temperature and salinity at standard depths, deductions concerning flow can also be made directly from the observed distributions of these water properties. Reasonable confidence may be placed in the interpretation of the circulation, particularly when the direction of flow suggested from the distribution of properties supports the calculated geostrophic currents. The following items are discussed: features of the distributions of salinity, temperature, and dissolved oxygen; changes in these properties near the bottom along the continental terrace; and water mass movements implied by temperature-salinity relationships.

SALINITY

Throughout most of the Subarctic Region, the salinity structure consists of three distinct permanent zones: (1) an isohaline upper zone, which extends from the surface to about 100 m.; (2) a halocline, in which the salinity increases about 1‰ between 100 and 200 m.; and (3) a lower zone, in which the salinity gradually increases with depth. The mechanism for the maintenance of this structure was discussed by Dodimead et al. (1963).

Perhaps the most striking changes in the distribution of properties within the coastal areas occur in the salinity distribution in the upper zone and are due to the intrusions of fresh-water runoff from coastal rivers. Various authors have attempted to distinguish oceanic and coastal water on the basis of the salinity distribution near the surface. In the North Pacific Ocean, Doe (1955) used the 32.5‰ isohaline as the boundary between offshore and coastal water masses in the upper zone; Dodimead et al. (1963) defined the extent of a coastal domain by the 32.4‰ isohaline; and Budinger et al. (1964) suggested the Columbia River effluent could be traced by salinities less than 32.5‰. Good agreement has thus been reached concerning a definable boundary be-

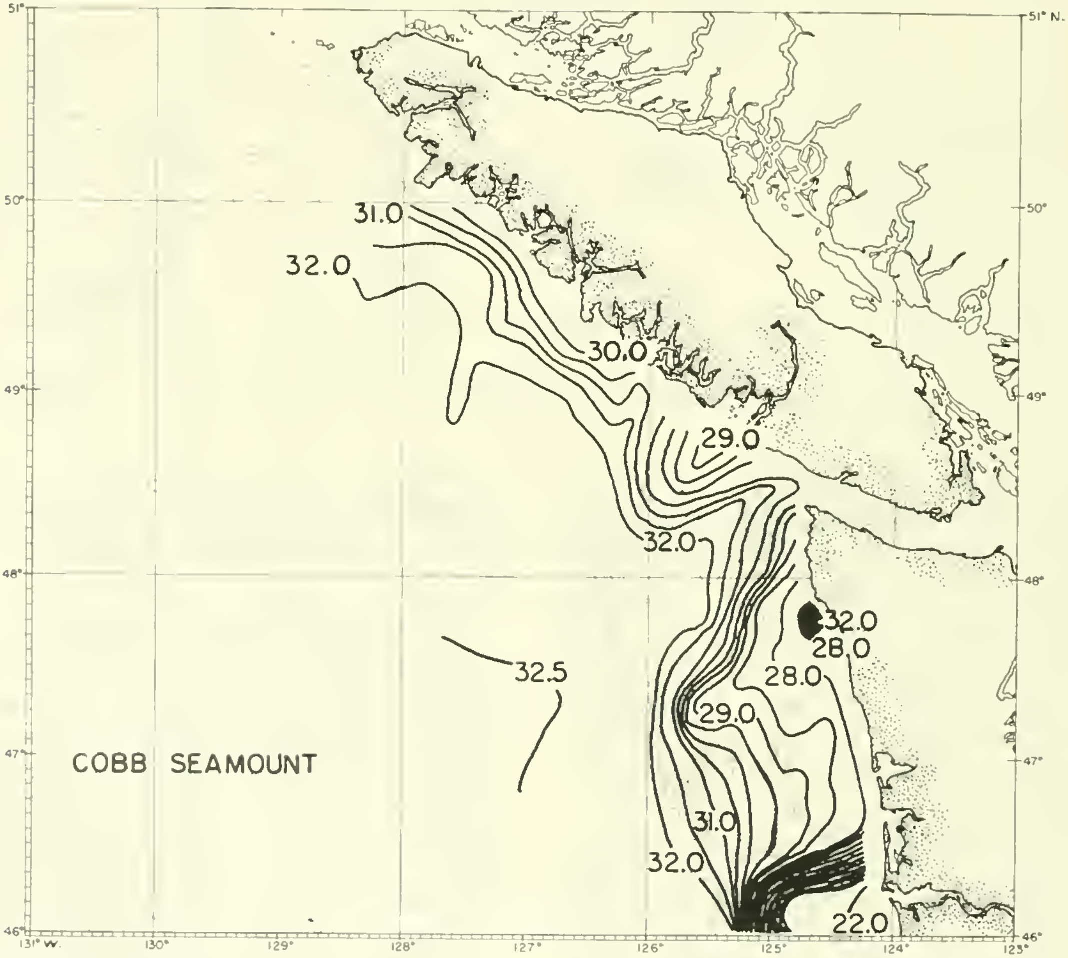


FIGURE 9.—Surface salinity (‰), spring 1963. (The 183- and 1,829-m. depth contours are shown.)

tween oceanic and coastal water, and the effects of dilution have been shown to extend over several hundred kilometers from shore (Favorite, 1961). Sharp gradients, or fronts, found closer to shore, however, are more interesting and much more complex.

The distribution of surface salinity during spring showed that the 32.5‰ isohaline approached within 160 km. of shore off the coast of Washington, but the most significant feature was the front associated with the 32.0‰ isohaline (fig. 9). The controversy regarding the precise definition of the term front in oceanographic usage has been discussed by Griffiths (1965). Front is used here in the sense that Cromwell and Reid (1956) defined the term, ". . . a band along the sea surface across which the density changes abruptly." The change of surface temperature near the front was not appreciable compared with the salinity change; thus the density change at the front was dominated by the relatively sharp decrease in surface salinity. Although no particular isohaline appeared to define the exact extent of the front throughout the area, gross changes in the position of the front may be seen by tracing the extent of the 32.0‰ isohaline. The largest gradient of surface salinity was about 80 km. from shore near lat. 46° N. where the front was apparently being maintained by effluent less was 22‰ from the Columbia River. The maximum seaward extent of the 32.0‰ isohaline was 112 km. near lat. 47° N.; at lat. 48° N. it had decreased to 64 km., and all along the coast of Vancouver Island it was confined to within 48 km. of shore. It is not clear whether the large tongue of dilute water off the central coast of Washington was a remnant of water from the Columbia River which had proceeded north along the coast during the winter or if it came directly from the Strait of Juan de Fuca. A patch of relatively high salinity water (> 32.2‰) about 11 km. seaward of Hoh Head indicated an area of local upwelling.

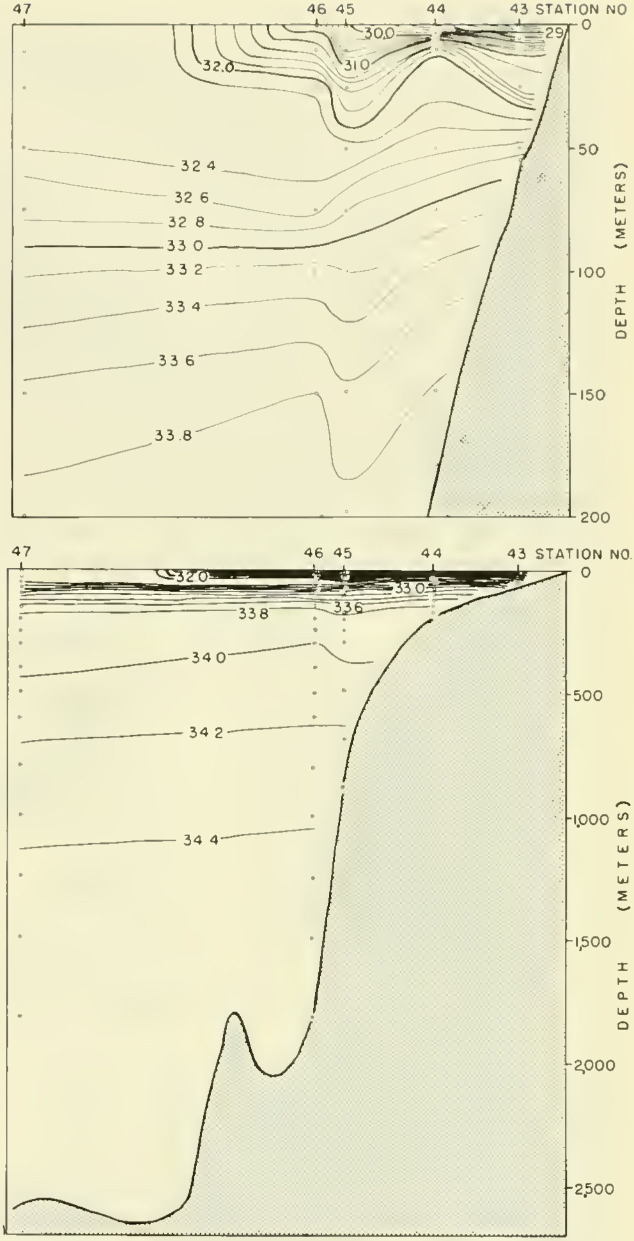


FIGURE 10.—Vertical sections of salinity (‰), 0 to 200 m. and 0 to 2,500 m., along Willapa Bay line, spring 1963.

A vertical section of salinity extending seaward from Willapa Bay illustrates the major changes in salinity with depth and distance from shore during spring (fig. 10). Dilute water of less than 32.0‰ in which the isolines were closely spaced, appeared to protrude seaward in the form of a tongue. Although the 32.0‰ isohaline that occurred at the leading edge of this tongue underwent large fluctuations in its seaward extent along the coast, the nearly constant depth of the 32.0‰ isohaline near shore shows that the major effect of the dilution off the coast of Washington was limited to the upper 30 to 40 m. Offshore, the three vertical zones characteristic of the Subarctic Region were present; although the boundaries between zones generally rose toward shore, the halocline and lower zone could be traced continuously inshore until they ended at the continental terrace.

Tully and Barber (1960) suggested that across the boundary of the halocline-lower zone 33.8 ± 0.1‰, only upward transfer of water existed; thus the depth of this surface forms the ultimate limit of downward transfer of water from the surface. Changes in properties below this surface are, therefore, primarily due to advection, not directly influenced by seasonal changes near the surface. The 33.8‰ surface was about 170 m. deep offshore but rose to about 130 m. near the 183-m. depth contour.

A horizontal section of salinity at 200 m. during spring showed uniform values of salinity just below the halocline; the range was from about 33.86‰ to 33.93‰ (fig. 11) —a marked contrast to the range of surface salinity, 22.0‰ to 32.5‰. A second important feature was the tongue of relatively high salinity (> 33.92‰) which appeared to point northward near the 1,829-m. depth contour off Willapa Bay. Although many of the features in the coastal area during the fall were similar to those during the preceding spring, important changes occurred near the surface between spring and fall. The salinity front was consistently nearer shore, 48 km. to 64 km. (fig. 12). The tongue of dilute water

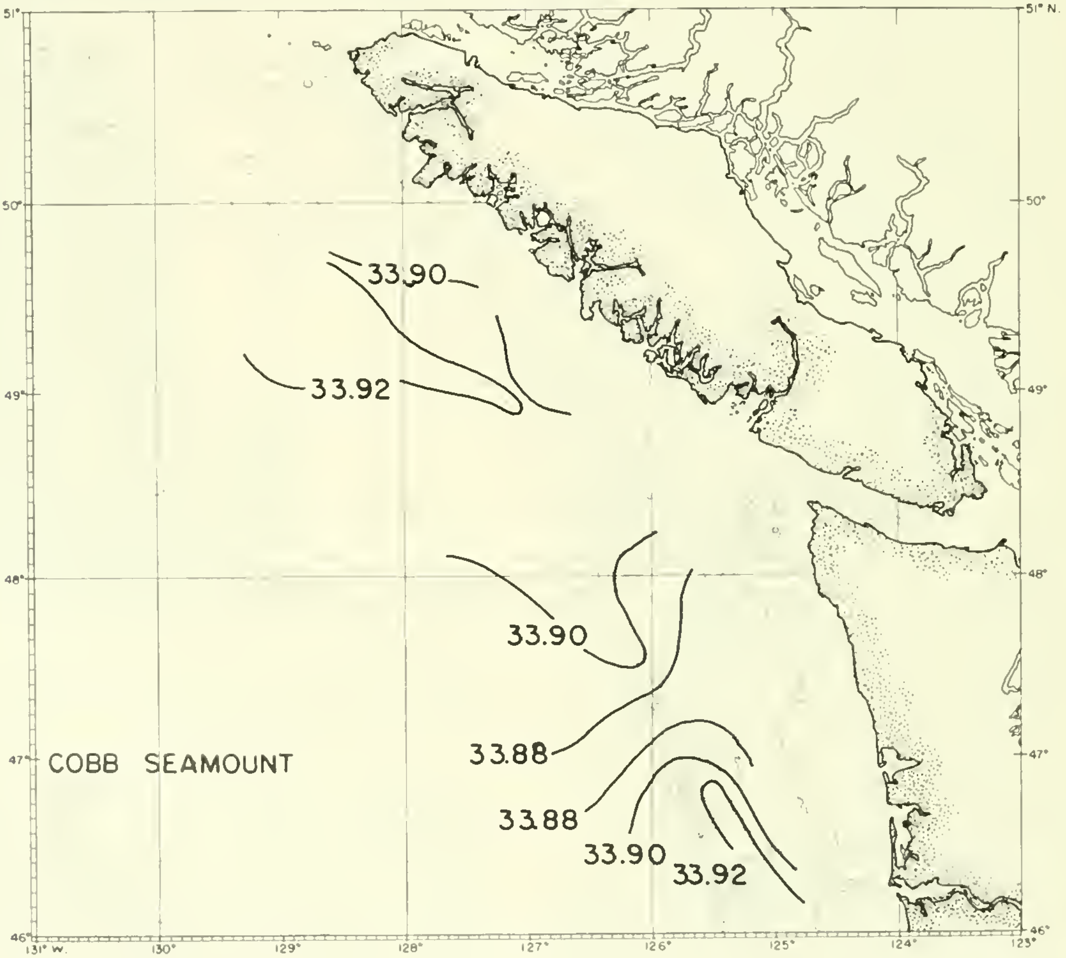


FIGURE 11.—Salinity (‰) at 200 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

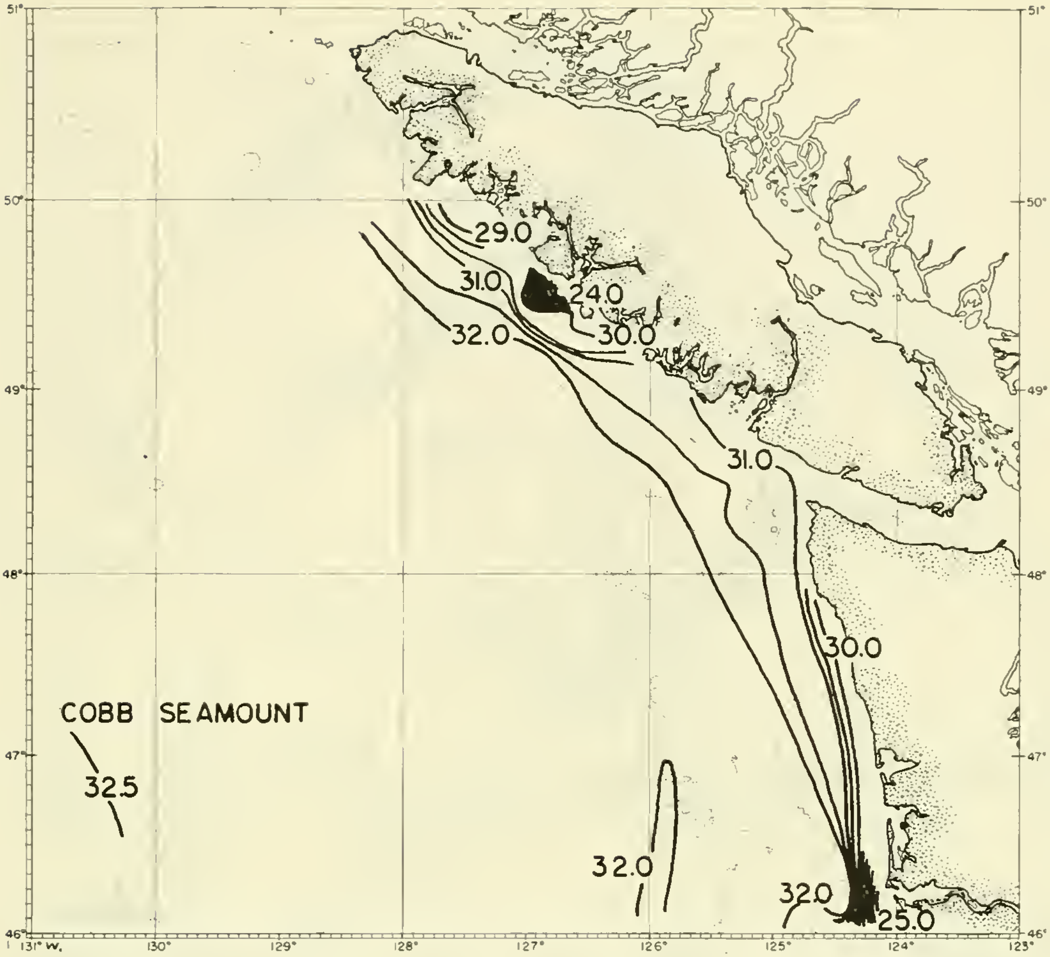


FIGURE 12.–Surface salinity (‰), fall 1963. (The 183- and 1,829-m. depth contours are shown.)

which had protruded twice as far seaward from the coast of Washington during the spring was absent in the fall. The 32.5‰ isohaline had shifted seaward from 160 km. to 400 km. by fall. Although the boundary between the halocline and lower zone fluctuated over a greater depth range during the fall, the major structural zones were again present and continuously defined along each section normal to shore. At 200 m. the maximum salinity increased to 33.96‰ between Willapa Bay and lat. 48° N. (fig. 13). The small tongue of greater salinity present during spring had enlarged to form a continuous ridge of high salinity along the coast with an axis about 140 km. from shore. This feature was more complex north of lat. 48° N. where the salinity decreased.

TEMPERATURE

In the Subarctic Pacific Region the water above the halocline begins to receive a net gain in heat in April and continues to warm into September (Dodimead et al., 1963). During the spring the surface-temperature gradient along the coast was uniform; temperatures from Vancouver Island to the Columbia River increased from 9.0° C. to 13.5° C. (fig. 14). Off the coast of Vancouver Island the surface isotherms were generally oriented northeast-southwest, normal to the shore, and showed no apparent relation to the surface-salinity front. Off the coast of Washington, however, the isotherms generally ran from north to south, parallel to shore. Their configuration agreed closely with the surface isohalines.

Vertical sections of temperature during

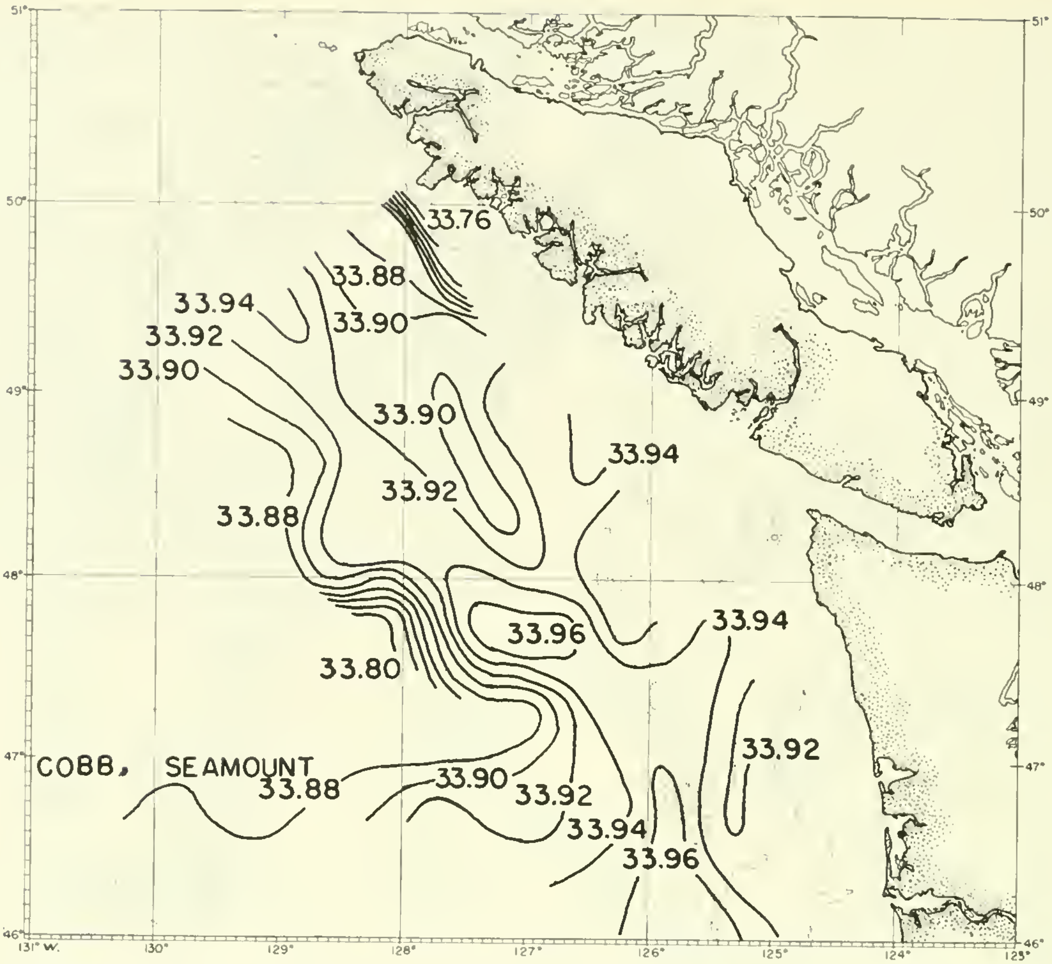


FIGURE 13.—Salinity (‰) at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

spring, one seaward from Cape Cook and the other seaward from Willapa Bay, illustrate the changes in temperature with depth and distance from shore as well as difference in temperature along the coast between the northern and southern parts of the area (fig. 15).

Characteristically the decrease of temperature with depth throughout the water column was inconsistent only within the halocline which contained sporadic inversions not in excess of 0.5° C. Below the halocline the temperature decreased logarithmically toward the bottom.

As was true with salinity, the most pronounced changes within the area took place in the upper layers. The dilute water near shore had a weak vertical gradient. Offshore from Cape Cook the upper 50 m. was isothermal, but toward the south, the magnitude of the seasonal thermocline increased between the surface and 30 m. Within the halocline off the Washington coast the isotherms rose toward shore over the Continental Shelf, but beyond the shelf they sloped slightly downward toward shore. The temperature increase from Cape Cook to Willapa Bay extended to a depth of at least 200 m. In the lower zone, the isotherms were relatively level. Although the variations of temperature at a particular depth below the halocline were small, the temperature distribution at 200 m. did show an unusual feature. A tongue of cold water (<6.8° C.) extended shoreward near the middle of Vancouver Island, interrupting a band of warmer water

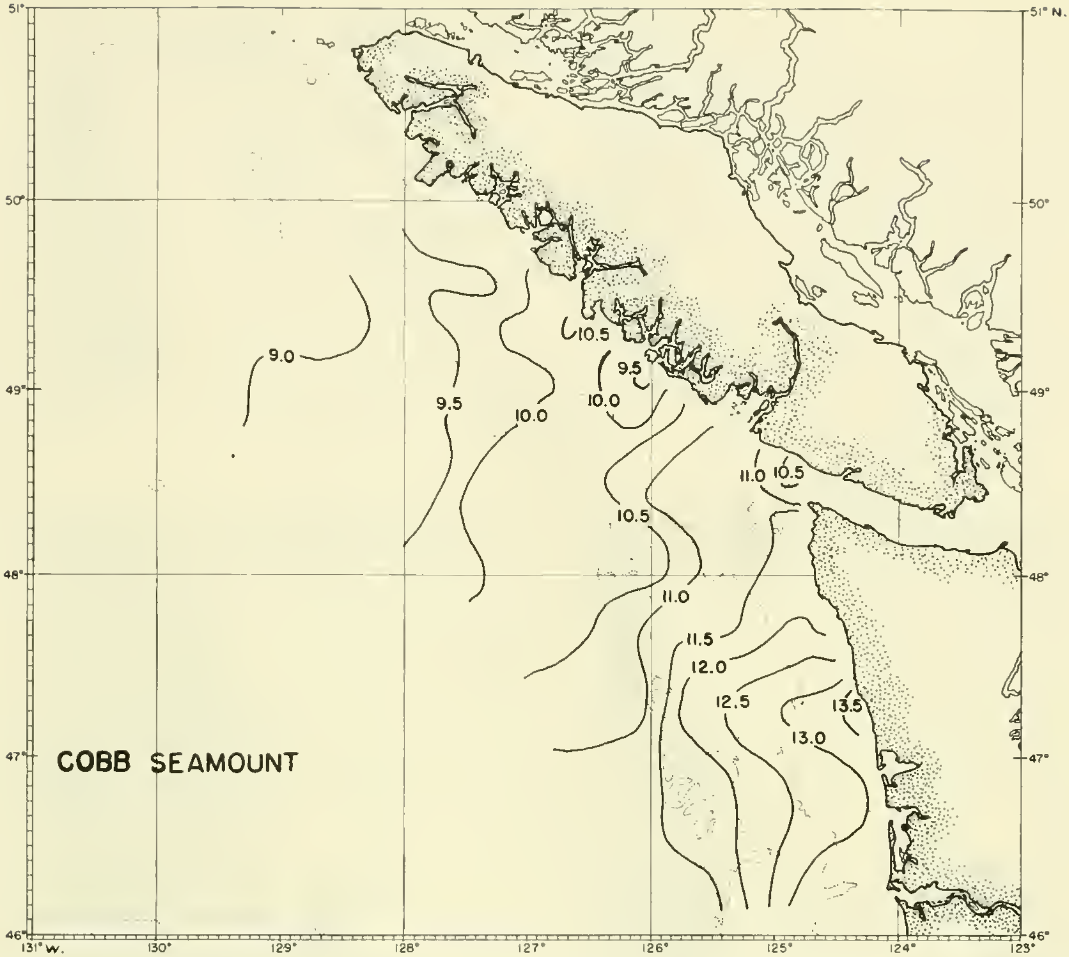


FIGURE 14.—Surface temperature (°C.), spring 1963. (The 183- and 1,829-m. depth contours are shown.)

(>7.2° C.) near the 1,829-m. depth contour (fig. 16).

Differences between temperatures during spring and fall were most pronounced above the halocline, in the zone affected by seasonal heating. Significant changes also occurred, however, within the lower zone which is not influenced directly by the seasonal heating; changes in circulation are implied.

Although the gradient of the surface temperature between northern Vancouver Island and the Columbia River was the same during each season, temperatures were generally 1.0° C. higher at each location during the fall (fig. 17). The most pronounced changes were near shore. During spring, warming was appreciable only near the surface in the dilute water off the coast of Washington, but in the fall the water was distinctly warmer over the entire Continental Shelf than offshore. The resulting temperature distribution shows a tongue of warm water extending northward along the coast and the maximum temperature along any line normal to shore near the edge of the Continental Shelf.

Comparison of fall and spring conditions along the same two vertical sections indicated many differences and similarities with depth and distance from shore. The most pronounced differences were in the upper 70 m. In contrast to the gradual decrease of temperature seaward during spring was the presence of two maxima during the fall—one at the surface near the edge of the Continental Shelf and the

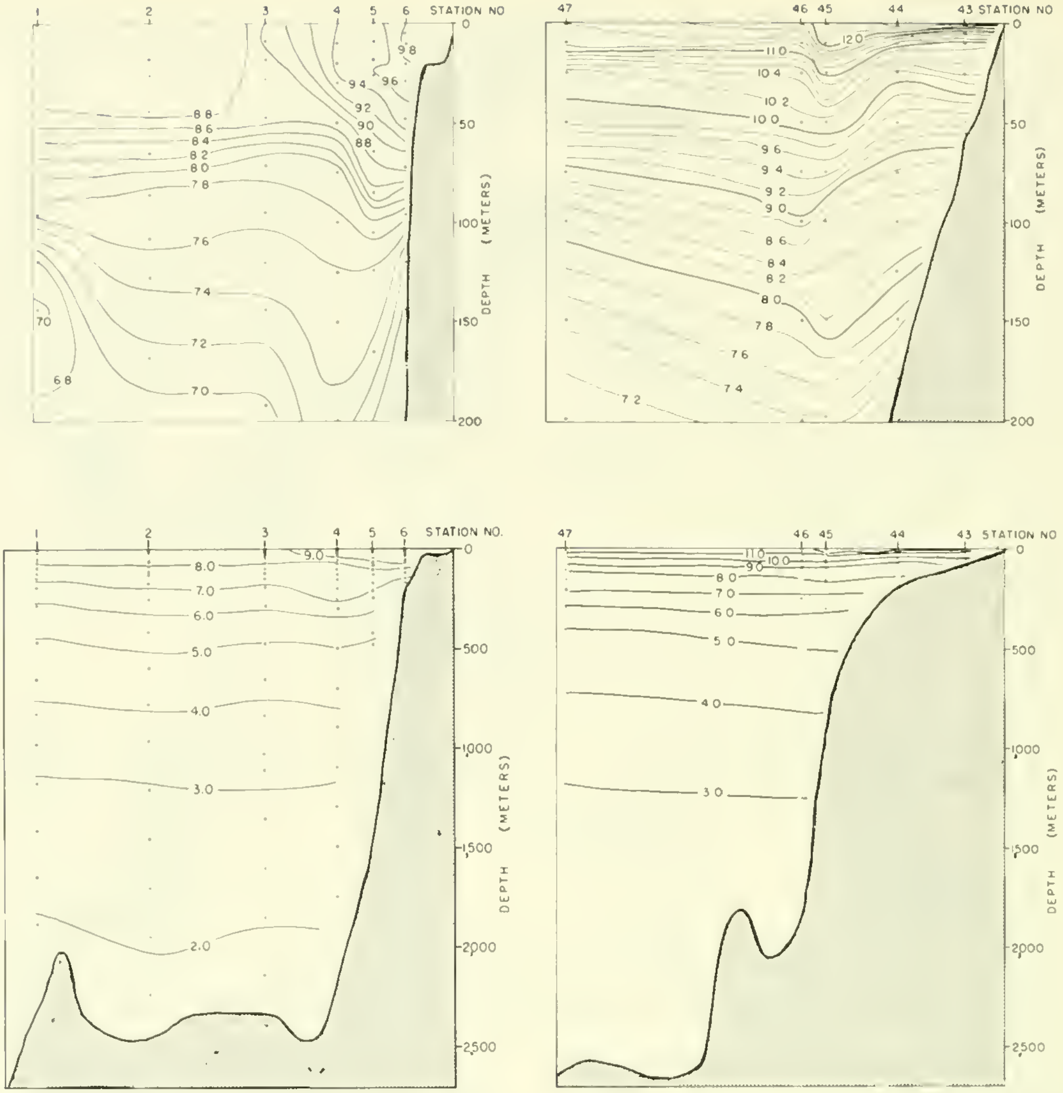


FIGURE 15.—Vertical sections of temperature (°C.), 0 to 200 m. and 0 to 2,500 m., along Cape Cook and Willapa Bay lines, spring 1963.

other at depth between 20 and 50 m. near shore. Apparently both maxima resulted from surface cooling and vertical mixing which had affected only the dilute water in the upper 20 m. Seaward of the salinity front, the upper 50 m. of the water column was isothermal off Cape Cook during both seasons. Southward of Cape Cook the magnitude of the thermocline again increased but by fall had deepened from the range 0 to 30 m. to between 50 and 70 m. in the top of the halocline. Temperature inversions were more frequent in the fall within the halocline, and the near-shore isotherms showed a slight depression or convergence. Vertical sections normal to shore during fall as in the spring showed the logarithmic decrease of temperature with depth and the level isotherms in the lower zone extending seaward from the Continental Slope.

Despite this general uniformity in temperature structure, minor changes did occur in the temperature distribution at 200 m. (fig. 18). The tongue of warmer water (> 7.2° C.) noted during spring changed: it became continuous along the coast, occupied a much larger area, and had a greater maximum temperature dur-

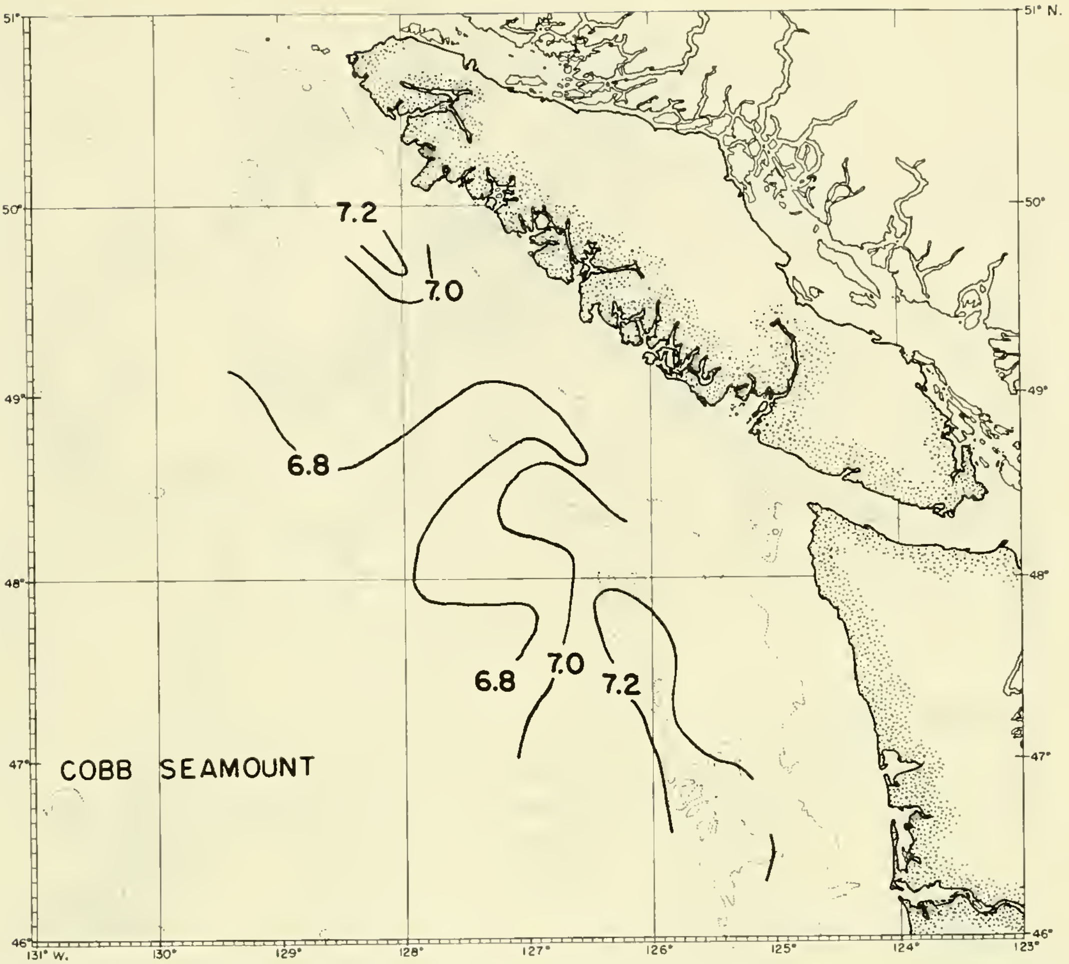


FIGURE 16.—Temperature (°C.) at 200 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

ing fall—7.6° C. Although this increase in temperature between spring and fall was slight, it may be significant compared with the small range of values at 200 m. The association of the warm water near the coast of northern Vancouver Island with the lowest salinity values implied a local convergence. Offshore the cold water was also of low salinity. The warm water off the coast of Washington near the 1,829-m. depth contour, however, was associated with the high-salinity ridge; a significant change in water mass is indicated.

DISSOLVED OXYGEN

The distribution of dissolved oxygen during the spring was obtained only over the continental terrace between the depths of 55 m. and 1,829 m. As with the distributions of temperature and salinity, the sharpest vertical gradient occurred within the halocline. Below the saturated or mixed layer, about 50 m. deep, values decreased sharply to about 300 m. Below 300 m., concentrations decreased gradually to a minimum near 900 m., below which values gradually increased toward the bottom.

Samples obtained at each station during the fall permit comparison of conditions near shore and offshore. The vertical section off Willapa Bay shows the complex distribution of dissolved oxygen in the upper 300 m. (fig. 19). Deeper isolines were relatively level and the oxygen minimum near 900 m. extended offshore without significant change in depth. The isolines within the upper 300 m. usually fol-

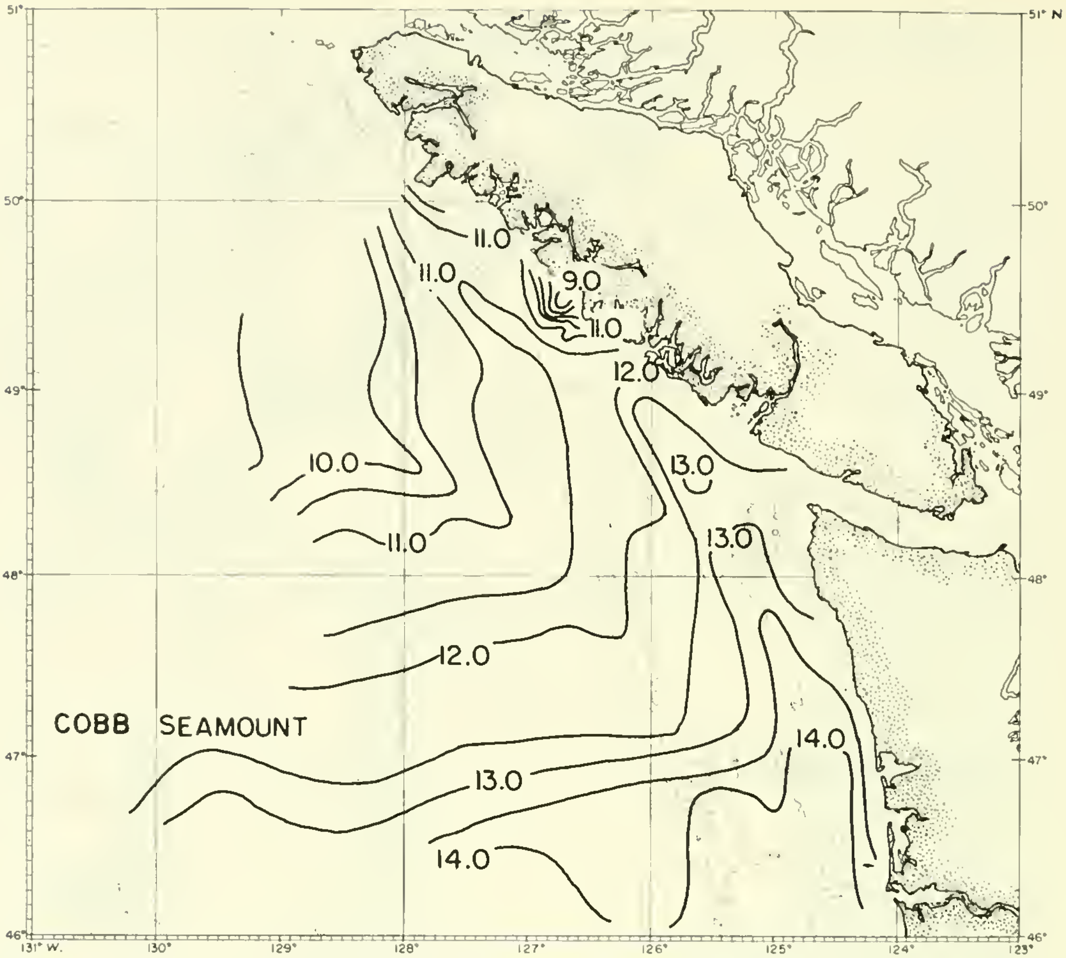


FIGURE 17.—Surface temperature (°C.), fall 1963. (The 183- and 1,829-m. depth contours are shown.)

lowed the configuration of the isohalines or isotherms, but were inclined generally upward toward shore. The rise reflected lower oxygen values near shore during spring and fall; minor inversions of dissolved oxygen were more frequent during fall, just below the bottom of the halocline near 200 m. A plot of dissolved oxygen at 200 m. during the fall (fig. 20) showed that this band of low oxygen concentration (< .20 mg. at./l.) was continuous along the entire coast over the Continental Slope and closely followed the high-salinity ridge (fig. 13).

Comparison of fall conditions with those over the Continental Slope during the preceding spring indicated that oxygen values at 200 m. had decreased on the average, by about 0.05 mg.at./l. If we assume that the seasonal change in biological utilization of dissolved oxygen was negligible, this decrease in dissolved oxygen concentration corroborates the change in water-mass characteristics between spring and fall previously indicated by the increase in temperature and salinity at 200 m. off the coast of Washington.

CONDITIONS NEAR THE BOTTOM

To determine changes in salinity, temperature, and dissolved-oxygen concentrations at a particular depth close to the sea floor along the continental terrace, samples were obtained as near the bottom as feasible—55 m., 183 m., 914 m., and 1,829 m. along each of the nine lines normal to shore. At the 55-m. and 183-m. sta-

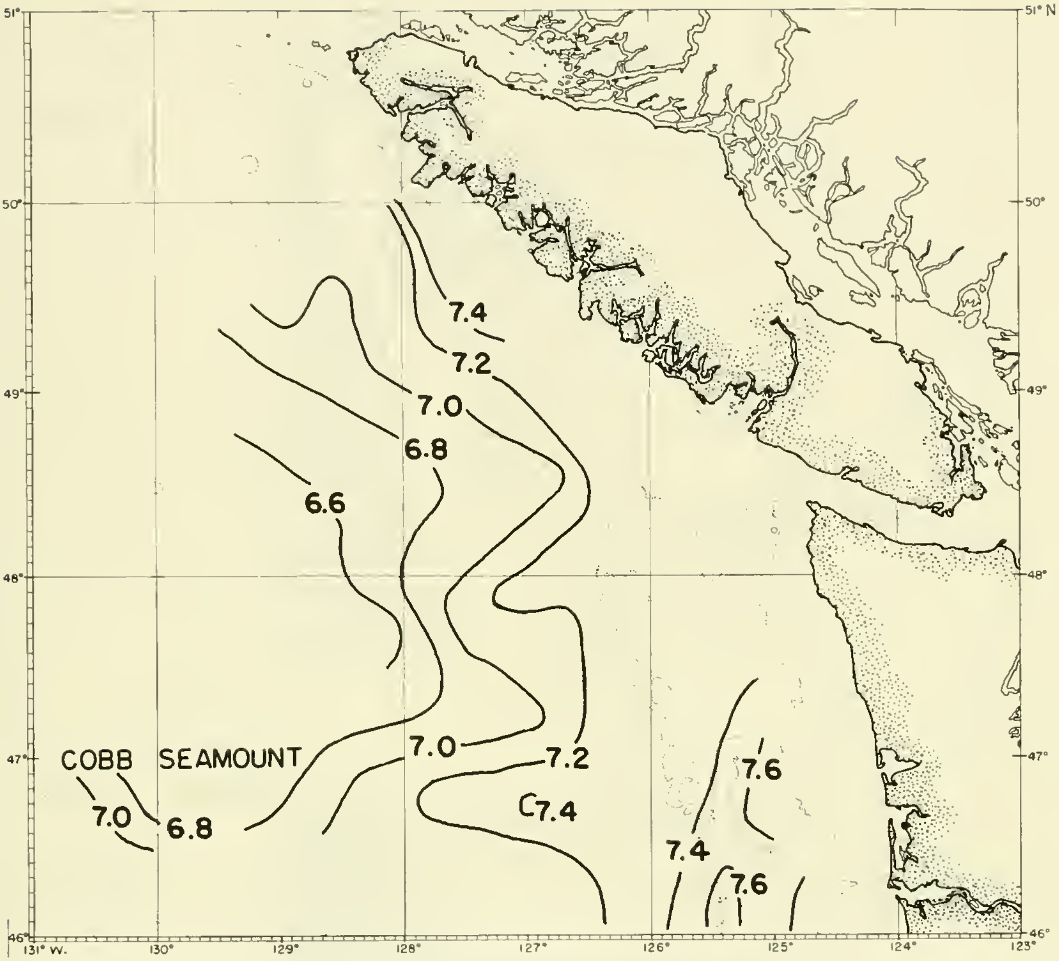


FIGURE 18.—Temperature (°C.), at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

tions, Nansen bottles were tripped 5 m. from the bottom by two methods. In the first method, the Nansen bottle is placed 5 m. above a weight suspended on the end of the wire, and the bottle is tripped by a messenger when a change in wire tension indicates the weight is striking the bottom. In the second method, a Nansen bottle attached to a tripping mechanism is reversed when a weight suspended 5 m. below the device strikes the bottom. Although agreement of results from both methods was good, values obtained by the first method were used for most stations. Because of the limited depth range of the vessel's echo sounder (about 550 m.) and the inability to detect the bottom by wire tension at great depths, the locations of the 914-m. and 1,829-m. stations were determined from charted depths; thus, the interval between the deepest bottle and the bottom depended upon the accuracy of the charted soundings and the vessel's position.

The spring values of salinity and temperature near the bottom varied most at shallow depths along the Continental Shelf and were uniform along the Continental Slope (fig. 21). At 55 m. salinity values were uniform between 31.9‰ and 32.0‰ north of the Strait of Juan de Fuca, but increased off Washington. The maximum of 33.4‰ was near the mouth of the Columbia River. The range of temperature values at 55 m. was about 1.0° C. The minimum value occurred off the Columbia River. The maximum salinity and minimum temperature indicated that water which is

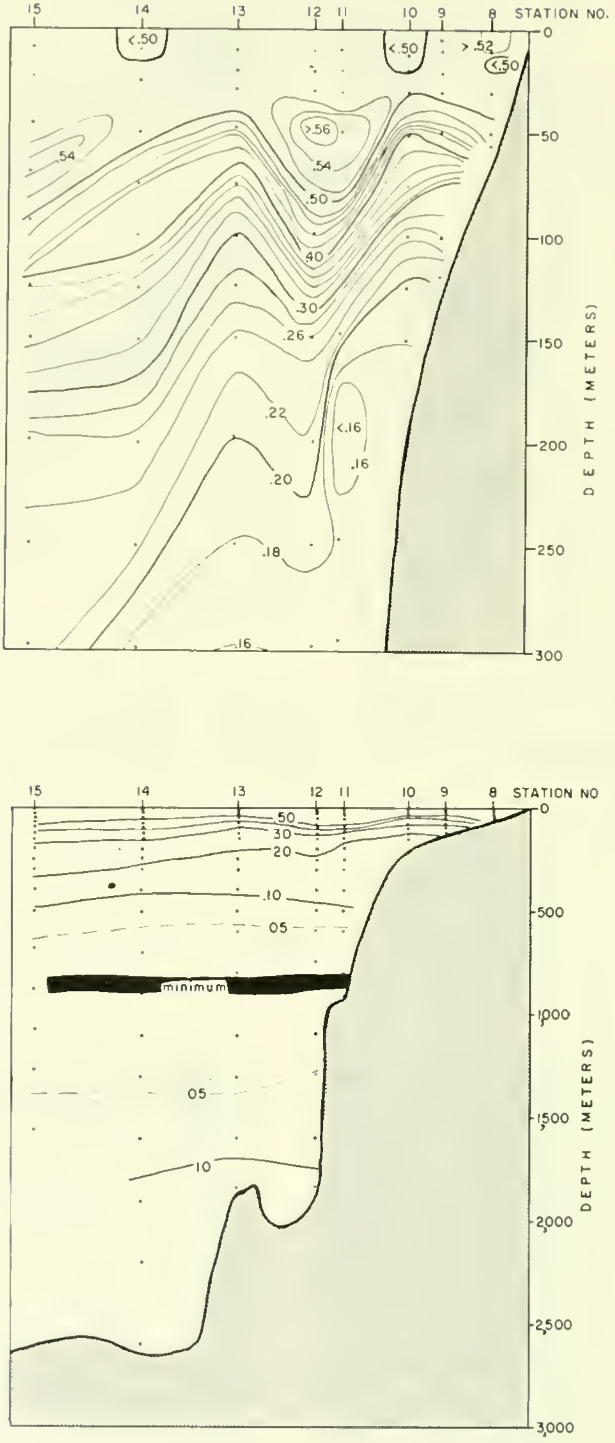


FIGURE 19.—Vertical sections of dissolved oxygen (mg.at./l.), 0 to 300 m. and 0 to 3,000 m., along Willapa Bay line, fall 1963.

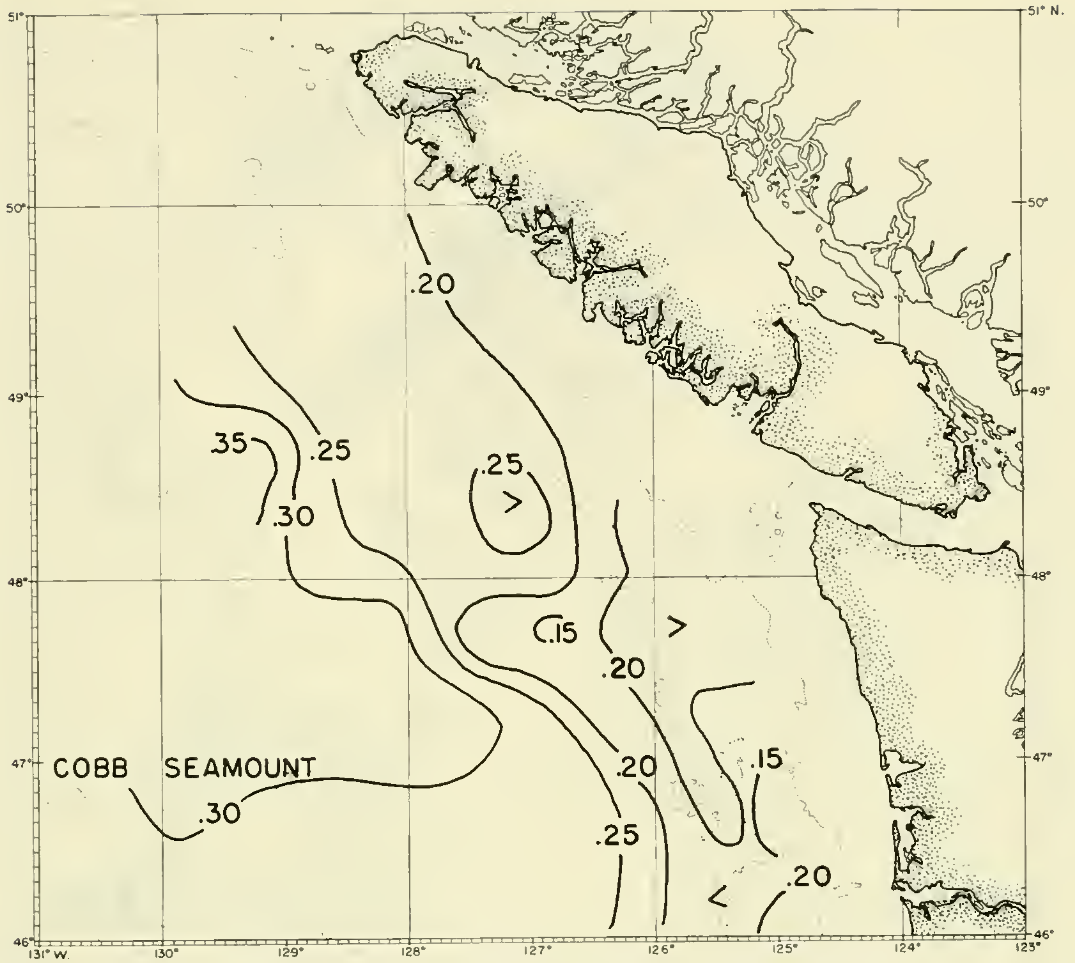


Figure 20—Dissolved oxygen (mg.at./l.) at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

normally found at a greater depth had moved shoreward in this area. Conditions near the bottom were reversed from those at the surface where the salinity was at a minimum and the temperature was at a maximum. At 183 m. the range of salinity was much smaller—between 33.67‰ and 33.95‰ — but the range of temperature at 183 and 55 m. was the same, 1.0° C. The salinity did not vary significantly along the coast and temperatures increased only slightly toward the south—about 0.1° C. Upwelling, therefore, was not taking place at 183 m. The range of values continued to decrease with depth. Changes in salinity ranged from 0.08‰ at 914 m. to 0.07‰ at 1,829 m., and differences in temperature ranged from 0.15° C. at 914 m. to 0.10° C. at 1,829 m. These minor variations indicated no significant change in salinity or temperature near the bottom along the Continental Slope during spring between the Columbia River and Cape Cook.

Values of dissolved oxygen near the bottom at 55 m. during spring were lowest off the mouth of the Columbia River (fig. 22). This situation appeared to corroborate the upwelling of deeper water, although biological utilization may have contributed to the low values. Oxygen, like salinity and temperature, followed no significant trend at a particular depth along the Continental Slope.

At 55 m., values of salinity, temperature, and dissolved oxygen in the fall were significantly different from those during spring.

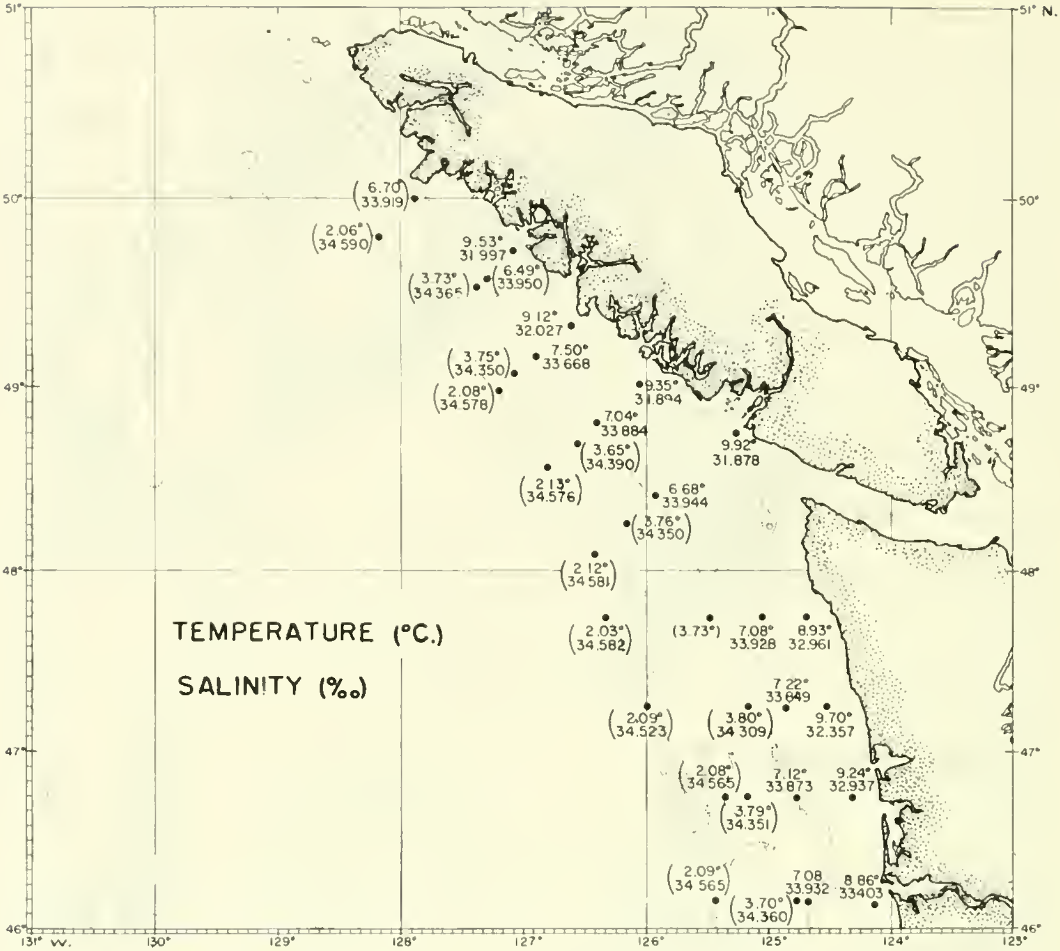
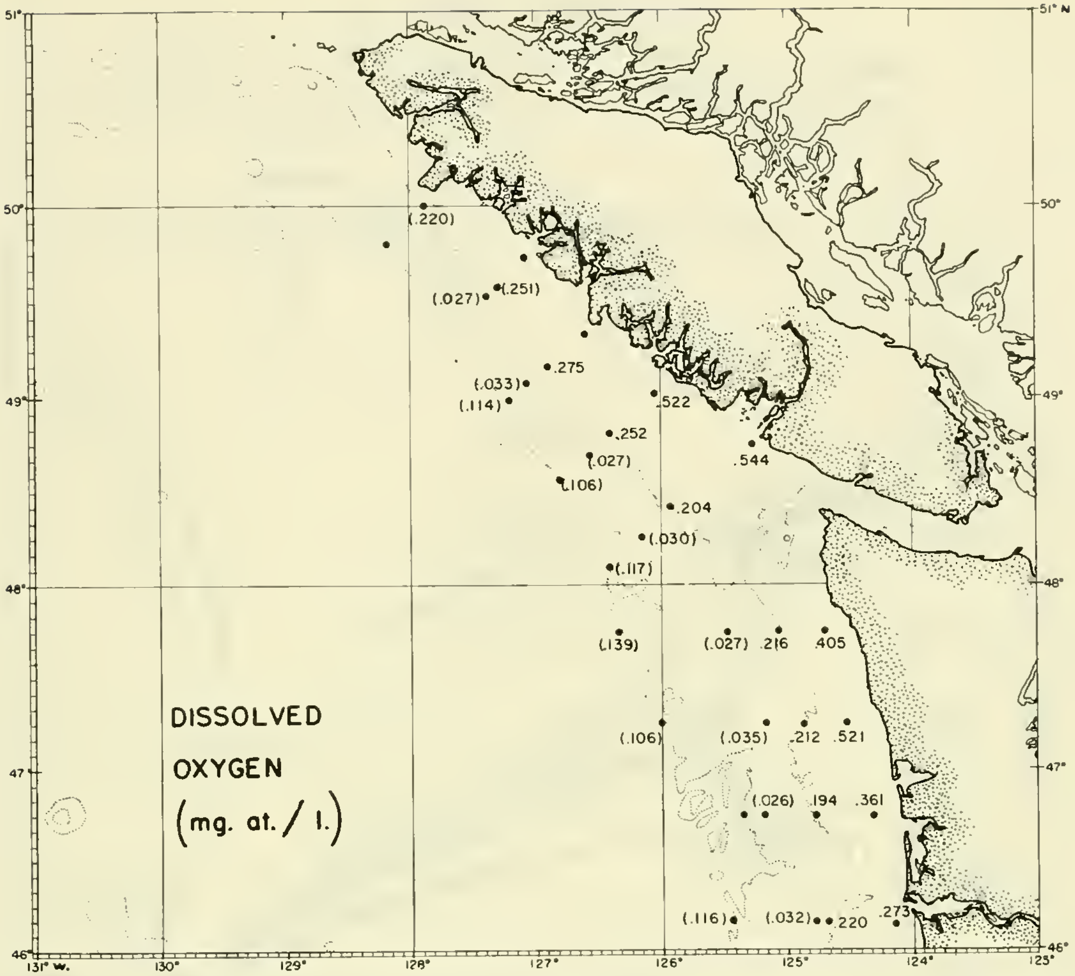

TEMPERATURE (°C.)
SALINITY (‰)
51°
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
(6.70 33.919)
(2.06° 34 590)
9.53° 31 997
(6.49° 33.950)
(3.73° 34 365)
9 12° 32.027
7.50° 33 668
(3.75° 34.350)
(2.08° 34 578)
9.35° 31.894
7.04° 33 884
(3.65° 34.390)
9.92° 31.878
(2 13° 34.576)
6 68° 33.944
(3.76° 34 350)
(2 12° 34 581)
(2.03° 34.582)
(3.73°)
7.08° 33.928
8.93° 32.961
7 22° 33.849
(2.09° 34.523)
(3.80° 34 309)
9.70° 32.357
(2.08° 34 565)
7.12° 33.873
9.24° 32.937
(3.79° 34.351)
(2.09° 34 565)
7.08 33.932
8 86° 33403
(3.70° 34.360)

Figure 21.—Temperature (°C.) and salinity (‰) near the bottom at 55, 183, 914, and 1,829 m. along the continental terrace, spring 1963. (The 183- and 1,829-m. depth contours are shown, and the values in parentheses are interpolated.)

Thus, more uniformity of salinity values — range from 31.6‰ to 32.3‰ — indicated absence of upwelling. By fall, temperatures at 55 m. had increased 3° C. off Vancouver Island, and 4° to 6° C. off the Washington coast. The increase was about 0.6° C. even at 183 m.

DISTRIBUTION OF WATER MASS BELOW 200 METERS

Analysis of distribution of temperature, salinity, and dissolved oxygen indicated significant changes in characteristics of water mass in near-shore areas and also between seasons. Water masses of different character conventionally have been defined by the temperature vs. salinity (T-S) curve plotted from serial oceanographic data (Sverdrup et al., 1942). All T-S curves from spring data were grossly similar; each had a characteristic s-shape and occupied a narrow envelope. The T-S curves of stations farthest offshore were consistently displaced downward toward the left, however. Waters here were colder and less saline than near the coast. The T-S curves from 10 stations within 500 km. of shore along the Willapa Bay-Cobb Seamount line during fall illustrate this displacement (fig. 23). The heavy curves on the lower and right-hand sides are general curves that represent the extreme water masses in the North Pacific Ocean—the Subarctic and Equatorial Pacific Water Masses; they indicate that the coastal water is a mixture of two water masses. The separation


51°
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DISSOLVED
OXYGEN
(mg. at. / l.)

FIGURE 22.—Dissolved oxygen (mg.at./l.) near the bottom at 55, 183, 914, and 1,829 m. along the continental terrace, spring 1963. (The 183- and 1,829-m. depth contours are shown, and values in parentheses are interpolated.)

between the offshore water mass that intrudes from the west and the coastal water mass that intrudes from the south was not distinct at all depths. Near 200 m. three distinct groups of curves existed. Stations 11 to 13 near shore had the most southern characteristics; stations 16 to 19 offshore had the most northern characteristics; and stations 14, 15, and 20 in the center were intermediate between the coastal and offshore water masses. Below 400 m. the boundary between the coastal and offshore water masses was distinct and lay between stations 14 and 15, about 165 to 220 km. from shore.

The study of horizontal changes in the characteristics of water masses throughout the coastal area showed that the differences in temperature were greatest on the salinity surface 34.0‰. Dodimead et al. (1963) suggested that temperatures greater than 6.0° C. on this surface defined the extent of the California Undercurrent Domain which appeared to originate south of lat. 35° N. Their geostrophic calculations, however, indicated only a weak northward flow below 200 m. during 4 of the 5 summers in 1955-59. The temperature distribution on the 34.0‰ salinity surface during spring and fall of 1963 showed the isolines were predominantly parallel to shore although a tongue of warm water apparently entered the area over the Continental Slope from the south. The boundary between the coastal and offshore water masses was marked by a temperature gradient on the seaward side

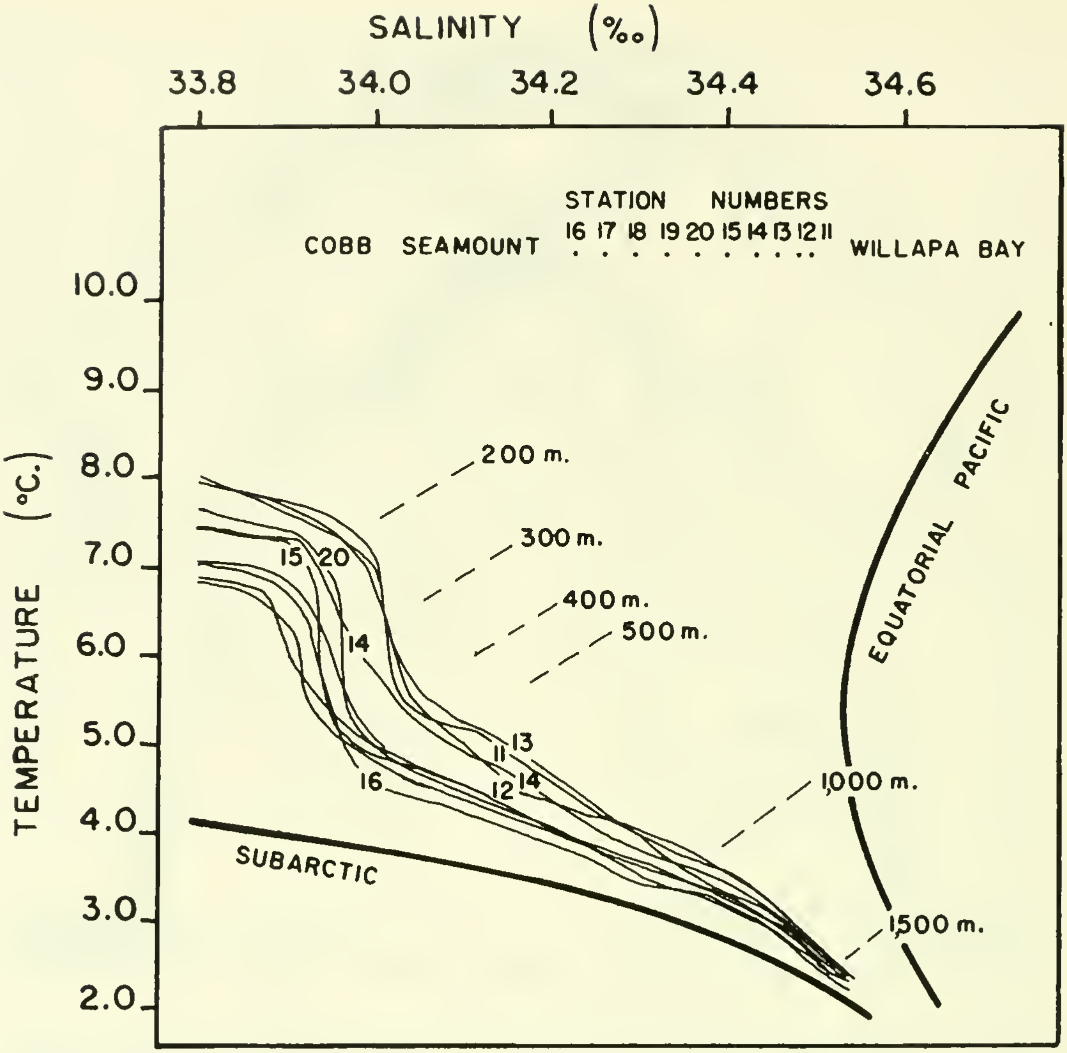

FIGURE 23.—Temperature vs. salinity curves for water of salinity greater than 33.8‰ between Willapa Bay and Cobb Seamount, fall 1963.

of the tongue. During spring the 6.0° C. isotherm was discontinuous off southern Vancouver Island (fig. 24) where the geostrophic currents indicated onshore movement (fig. 4). The distribution of temperature greater than 6.0° C. showed a band of more southern water about 40 km. wide seaward of the Continental Shelf.

The configuration of the isotherms on 34.0‰ surface was generally similar to the geostrophic currents at 200 m., and the southern water mass was located to the right (if one faces downstream), even when the current was southbound.

The greater area encompassed by the southern water (> 6.0° C.) off the coast of Washington during the fall suggests that the northward flow was greater during fall (fig. 25), but the increased flow was not reflected in the net volume transport.

A more quantitative approach to the description of the distribution of water masses along the Pacific Coast of the United States was made by Tibby (1941) who applied the method of Sverdrup and Fleming (1941) to data obtained by the *E. W. Scripps* in 1939.

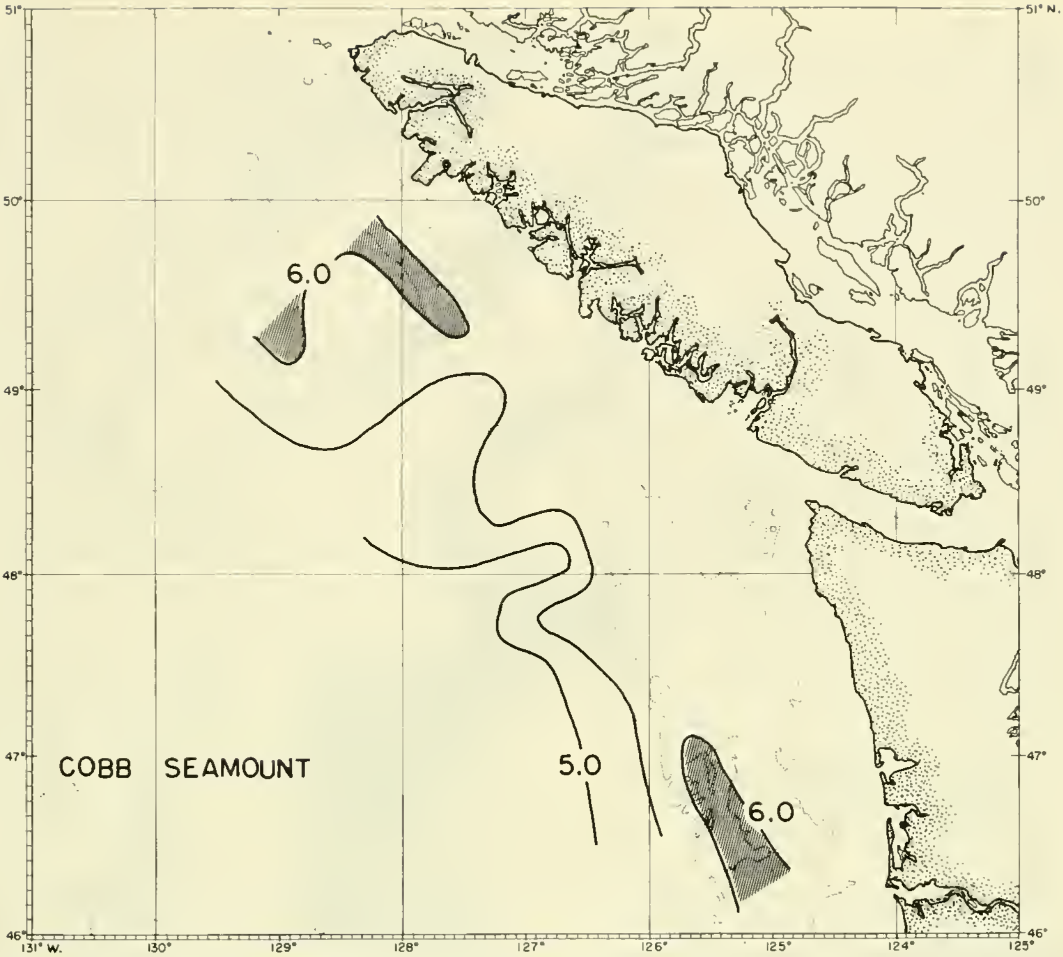

FIGURE 24.—Temperature (°C.) on salinity surface 34.0‰, spring 1963. Shaded portion is above 6.0° C. (The 183- and 1,829-m. depth contours are shown.)

He showed a relatively higher percentage of Equatorial Pacific Water to be present along the Pacific Coast near shore from lat. 25° N. to lat. 45° N. All vertical sections normal to shore showed a greater percentage of southern water toward the bottom and toward shore. The low percentages of southern water in the northernmost sections (between 20 and 40 percent) suggested increased mixing with Subarctic Water to the north.

The percentage of Equatorial Pacific Water off the Washington coast along lat. 46°45′ N. during the fall of 1963 agreed closely with Tibby's results (fig. 26). Because this location is 222 km. farther north than Tibby's most northern line, however, a slightly lower percentage was found. Percentages were not only relatively high near the bottom and near shore, but the high percentages between 200 m. and 400 m. immediately below the halocline extended offshore as far as 500 km. This situation resulted in a pronounced minimum, from 10 to 20 percent, between 600 and 900 m. Values increased sharply within 220 km. of shore. The depth of this minimum percentage of Equatorial Pacific Water coincided surprisingly well with the depth of the oxygen minimum. This determination of distribution of water masses suggests a change in circulation with depth; between 400 m. and 1,000 m., Subarctic Water may move onshore from the west; whereas, between 200 m. and 400 m. and between 1,000 m. and 1,300 m., southern water may move northward along the coast.

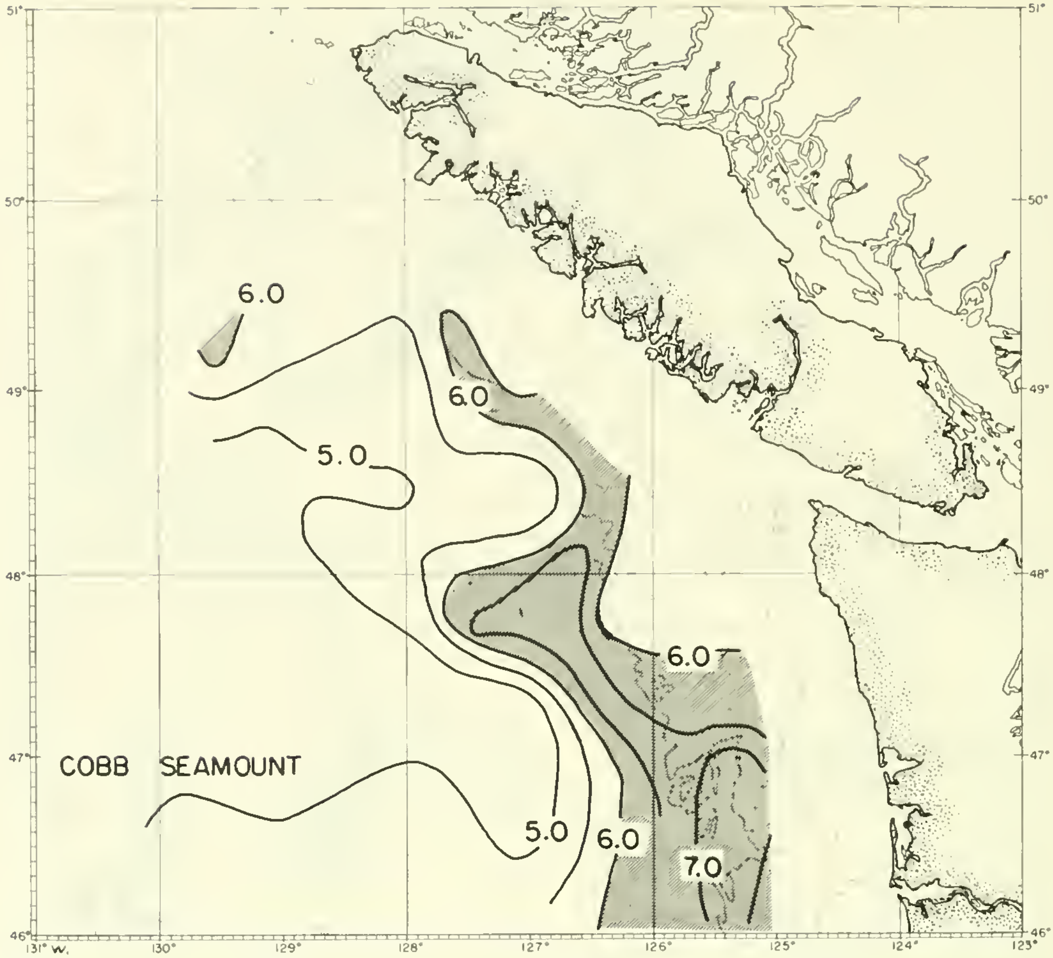

FIGURE 25.—Temperature (°C.) on salinity surface 34.0‰, fall 1963. Shaded portion is above 6.0° C. (The 183- and 1,829-m. depth contours are shown.)

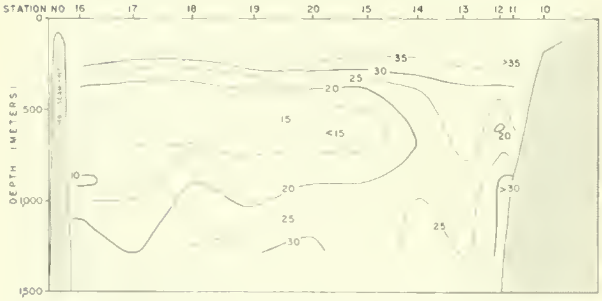

FIGURE 26.—Vertical section of the percentage of Equatorial Pacific Water for water greater than 33.8‰ between Willapa Bay and Cobb Seamount, fall 1963.

SIGNIFICANT OCEANOGRAPHIC FEATURES OF COASTAL WATER

Data obtained during the spring and fall 1963 at closely spaced stations along nine lines normal to shore between the Columbia River and Cape Cook, Vancouver Island, have permitted a description of the significant oceanographic features in the spring within 220 km. of the Vancouver Island and Washington coasts and changes that occurred by the succeeding fall.

Surface geostrophic currents, 0/1,500 db., were similar during both spring and fall. Offshore water flowed northeasterly toward the middle of Vancouver Island and then turned toward the northwest generally parallel to the coast. Eddies off the coast of Washington were such that the northward flow over the Continental Slope, perhaps the Davidson Current, did not appear to continue north of lat. 48° N.

Geostrophic currents, 200/1,500 db., followed the same direction as the surface currents, and showed maxima of subsurface velocity in the eddies off the Washington coast.

The net volume transport, based on a 1,500 db. reference level, was 3 x 10^6m.^{3}/sec. northward past Cape Cook during both spring and fall. A shoreward component of total transport 6.7 x 10^6m.^{3}/sec., was present in the spring, but by fall the transport had reversed to the seaward at 0.4 x 10^6m.^{3}/sec. Northward transport of 4 to 5 x 10^6m.^{3}/sec. occurred locally off the coast of Washington, but was associated with strong anticyclonic eddies which had nearly an equivalent southward transport. Although the existence of the California Undercurrent may be implied by the distribution of properties and supported by the direction of the geostrophic currents at 200 m., the Current did not appear to contribute more than 1 x 10^6m.^{3}/sec. to the net northward flow along the coast of Washington.

The most striking and permanent feature of the distribution of properties within the area was the surface salinity front which extended to a maximum distance of 112 km. seaward from the coast of Washington during the spring, but was confined within 64 km. of the coast in the fall. Vertical sections normal to the shore showed that the major structural features of salinity, temperature, and dissolved oxygen were consistent along each of the nine lines. The distribution of properties varied considerably above 200 m. within the main halocline, thermocline, and oxycline. Below 200 m. the range of values of salinity, temperature, and dissolved oxygen at a given depth was comparatively small. The major feature below the halocline was the nearly horizontal isolines of temperature, salinity, and dissolved oxygen along each vertical section. The concentration of dissolved oxygen had a pronounced minimum at about 900 m. throughout the study area. Minor variations at 200 m. in the fall indicated that a ridge of high-salinity water, also associated with high temperature and low dissolved oxygen, was especially well developed along the Continental Slope of Washington.

Samples obtained near the bottom confirmed the absence of any significant change in the salinity, temperature, or dissolved oxygen at a particular depth along the Continental Slope between the Columbia River and Cape Cook. Thus, the only significant variations in water properties occur in the upper 200 m.

The T-S curves indicated that a water mass of high salinity and high temperature was present over the Continental Slope. Off the coast of Washington the boundary between water masses of slightly different characteristics was distinct below 400 m. between 165 and 220 km. from shore. The more southern water mass near shore occupied a greater portion of the coastal area during the fall than in the spring. Although this implied an increase in northward flow at depth, the California Undercurrent, increased flow was not reflected in the net volume transport.

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SYSTEMATICS AND BIOLOGY OF THE BONEFISH, *ALBULA NEMOPTERA* (FOWLER)[1]

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ABSTRACT

This study is a review of the taxonomic status of the bonefish, *Albula nemoptera*, formerly placed in the genus *Dixonina*. Reasons for synonymizing *Dixonina* with *Albula* are discussed, and it is shown that *pacifica* is conspecific with *nemoptera*. The Atlantic and Pacific populations of *nemoptera* are compared with each other and with the common bonefish, *A. vulpes*. Presumed larval and juvenile stages of *nemoptera* are described and compared with those of *vulpes*. The ecology and distribution of *nemoptera* and *vulpes* is discussed.

Prior to 1911 the family Albulidae was known from several fossil forms and one living species, *Albula vulpes* (Linnaeus). Fowler (1911) described the second living species, *Dixonina nemoptera*, from a single specimen from Hispaniola. Eight years later a second specimen was recorded by Metzelaar (1919) from Venezuela and a third, from the Pacific coast of Mexico, by Myers (1936). A drawing of a specimen from the Pacific coast of Mexico identified as "*Albula vulpes*," was published by Kumada and Hiyama (1937). According to Walford (1939), apparently several specimens were available to these authors. Beebe (1942), on the basis of 19 specimens from Costa Rica, proposed the name "*Dixonina pacifica*" for the Pacific coast population. The third Atlantic record (Rivas, 1952) was based on two specimens from Jamaica. Recently Caldwell and Caldwell (1964) recorded, tentatively as "*Albula vulpes*," 14 larvae and juveniles from the Atlantic coast of Panama.

According to the literature, therefore, this apparently rare species of albulid was hitherto known only from four Atlantic records (7 larvae, 6 juveniles, and 4 adults) and the three Pacific records (21 specimens of which 14 are not traceable).

During its cruise No. 92, May 5 through June 17, 1964, the Bureau of Commercial Fisheries exploratory fishing vessel *Oregon* collected 21 adult specimens of *Albula nemoptera* along the Atlantic coast of Colombia. Nineteen of these are available for the present study (see materials and acknowledgments); one was deposited at the Santa Marta Marine Laboratory, Santa Marta, Colombia, and another at the Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory in Miami, Fla.

Additional specimens from the Atlantic and Pacific, not previously reported in the literature, were located in various institutions.

The fairly adequate material of *A. nemoptera*, now at hand, prompted this study, particularly because the most recent account of the species was based on a single specimen (Hildebrand, 1963) and the conclusions reached therein are open to question (Berry, 1964). In due fairness to the late S. F. Hildebrand, however, it should be remembered that his study was published 14 years after his death in 1949.

We performed this research at the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Pascagoula, Miss.

MATERIALS

This paper is based on 56 specimens (35 Atlantic; 21 Pacific) of *A. nemoptera* and 43 Atlantic specimens of *A. vulpes* from the

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[3] Present address: BCF Biological Laboratory, Beaufort, N.C.

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collections of the U.S. National Museum (USNM), Stanford University (SU), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum (LACM), University of California at Los Angeles (UCLA), University of Miami Institute of Marine Science (UMML), and University of Miami Ichthyological Museum (UMIM). This material is distributed as follows:

A. nemoptera (Atlantic).—Colombia: about 40 km. (22 nautical miles) NW. of Punta San Bernardo, USNM 199530 (3 adults), FMNH 66796 (2 adults); about 22 km. (12 nautical miles) WNW. of Puerto Colombia, USNM 199474 (6 adults), UMIM 5926 (2 adults); about 23 km. (13 nautical miles) NE. of Santa Marta, FMNH 66795 (2 adults), UMIM 5927 (2 adults); about 18 km. (10 nautical miles). WSW. of Puerto Colombia, UMIM 5925 (2 adults). Panama: Caledonia Bay, LACM 20467 (7 larvae, 4 juveniles), LACM 20468 (2 juveniles). Jamaica: Port Antonio, LACM 5802 (1 adult), UMIM 1028 (2 adults).

A. nemoptera (Pacific).—Mexico: Guerrero, Acapulco, USNM 75547 (1 adult); Sinaloa, Mazatlan Playa Camaron, UCLA W51-22 (13 young). Costa Rica: Potrero Grande, SU 46385 (5 young to adult); Gulf of Nicoya, Quepos, UCLA W54-55 (1 adult). Panama: Perlas Islands, Isla del Rey, Punta de Cocos, UCLA W53-285 (1 young).

A. vulpes (Atlantic.). — Florida: Monroe Co., Flamingo, Buttonwood Canal bridge, UMML 16775 (20 young); Dade Co., Miami, UMIM 5917 (2 adults). Bahamas; Cay Sal Bank, Cotton Cay, UNIM 5916 (7 adults). Cuba: Havana, estuary of Guanabo River, UMIM 758 (5 juvenile and young). Jamaica: Port Antonio, UMIM 5918 (1 adult). Colombia: St. Andrews Island, UMIM 5928 (8 larvae).

METHODS

Measurements and counts were made according to methods described by the senior author (Rivas, 1960) with the following modifications and additions. Standard length was measured from the tip of the snout (not the upper lip) to the middle of the caudal base. Prepectoral length was measured from the tip of the snout to the insertion of the appressed left pectoral fin. Head length is the longest distance between the tip of the snout and the margin of the left opercular membrane. Mandible length comprises the distance between the anterior tip of the dentary and the posterior tip of the left articular. Preoral length is the median ventral distance between the tip of the snout and the anterior tip of the dentary with the mouth closed. Body depth was measured at the origin of the dorsal fin. Dorsal and anal fin heights were measured from the origin of the erect fin to the upper tip. Last dorsal and last anal ray lengths were measured between the end of the fin base and the tip of the ray. All the dorsal and anal rays were counted, including the anteriormost short, closely approximated elements. The last two dorsal and anal rays were counted separately. All counts were made from the fish's left side. All pectoral and pelvic rays and all branched caudal rays were counted. All pored scales were counted including those beyond the caudal base. The scales above the lateral line were counted downward and backward from the dorsal fin origin to, but not including, the lateral line. Those below the lateral line were counted upward and forward from the anal fin origin to, but not including, the lateral line. Only the modified predorsal scales, along the midline of the back anterior to the dorsal fin, were counted. The scales around the caudal peduncle were counted at the region of the least depth. All the gill rakers on the first arch were counted, including rudiments; the count for the lower limb includes the gill raker at the angle. All branchiostegal rays were counted. The vertebral counts include the hypural.

GENERIC STATUS OF THE BONEFISH

Largely on subjective grounds the genus *Dixonina* Fowler (1911) is here considered as a synonym of the genus *Albula* Scopoli (1777).

The only two living species of the family Albulidae (*Pterothrissus* not included), *A. vulpes* and *A. nemoptera*, are much more closely related to each other than previously suspected. The differences between them are only of degree and not of the order that would merit generic separation (tables 1–11). Their great superficial similarity is further emphasized by

Table 1.—*Comparison of 21 Atlantic* Albula nemoptera *and 10* A. vulpes *of similar mean length on the basis of differential proportional characters (in thousandths of the standard length)*

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A−) negatively allometric]

Character	*A. nemoptera*		*A. vulpes*	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	234–341	289	204–387	293
Prepectoral length (A−)	270–301	286	255–280	268
Preanal length (A+)	824–847	836	835–856	844
Head length (I)	289–312	299	267–296	286
Maxillary length (I)	133–142	138	91–103	94
Mandible length (I)	118–128	123	83– 97	93
Preoral length (I)	43– 49	46	26– 35	29
Orbit diameter (I)	46– 53	50	52– 60	55
Caudal peduncle depth (I)	60– 68	63	70– 78	74
Dorsal base length (I)	173–190	183	138–176	154
Dorsal fin height (A−)	161–177	169	182–197	188
Last dorsal ray length (A+)	152–193	170	54– 56	60
Last anal ray length (A+)	80– 99	89	54– 65	58
Upper caudal lobe length (A−)	204–234	223	232–275	256
Lower caudal lobe length (A−)	187–208	200	216–254	239

Table 2.—*Comparison of 9 Atlantic and 7 Pacific specimens of* Albula nemoptera *of similar mean length on the basis of proportional characters (thousandths of the standard length)*

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A−) negatively allometric]

Character	Atlantic		Pacific	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	72–341	246	78–346	205
Predorsal length (A+)	464–490	479	473–513	489
Prepectoral length (A−)	278–301	288	267–294	283
Prepelvic length (A+)	558–602	589	570–610	586
Preanal length (A+)	806–847	829	814–838	830
Head length (I)	297–304	300	280–302	290
Snout length (I)	110–120	115	107–116	111
Maxillary length (I)	133–140	138	124–139	130
Mandible length (I)	119–128	123	111–129	118
Preoral length (I)	43– 49	45	39– 49	42
Orbit diameter (A−)	47– 68	53	46– 67	52
Interorbital width (I)	61– 69	65	61– 66	65
Body depth (A+)	178–199	190	165–208	184
Caudal peduncle depth (I)	60– 70	65	62– 68	66
Dorsal base length (I)	179–194	186	181–201	189
Anal base length (I)	51– 63	58	56– 66	59
Dorsal fin height (A−)	163–192	173	171–194	181
Anal fin height (I)	87– 94	90	88–105	98
Pectoral fin length (I)	142–152	147	141–161	151
Pelvic fin length (I)	114–136	121	120–130	125
Last dorsal ray length (A+)	39–178	150	45–175	130
Last anal ray length (A+)	49– 96	86	54–107	87
Upper caudal lobe length (A−)	204–234	222	217–237	237
Lower caudal lobe length (A−)	187–208	200	212–230	222

Table 3.—*Frequency distribution of dorsal and pelvic rays in* Albula nemoptera *and* A. vulpes

Species	Dorsal rays						Pelvic rays				
	No.	*18*	*19*	*20*	*21*	*Mean*	*8*	*9*	*10*	*11*	*Mean*
A. nemoptera (Atlantic)	28	----	----	3	25	20.9	----	28	----	--	9.0
A. nemoptera (Pacific)	21	----	----	4	17	20.8	1	20	----	----	9.0
A. vulpes (Atlantic)	39	10	29	----	----	18.7	----	3	35	1	9.9

Table 4.—*Frequency distribution of pectoral rays in* Albula nemoptera *and* A. vulpes

Species	Pectoral rays						
	No.	*15*	*16*	*17*	*18*	*19*	*Mean*
A. nemoptera (Atlantic)	28	-----	3	22	3	-----	17.0
A. nemoptera (Pacific)	21	2	4	10	4	1	16.9
A. vulpes (Atlantic)	35	-----	-----	2	20	13	18.3

Table 5.—*Frequency distribution of lateral line scales in* Albula nemoptera *and* A. vulpes

Species	Lateral line scales																				
	No.	*68*	*69*	*70*	*71*	*72*	*73*	*74*	*75*	*76*	*77*	*78*	*79*	*80*	*81*	*82*	*83*	*84*	*85*	*86*	*Mean*
A. nemoptera (Atlantic)	22	--	--	--	--	--	--	--	--	--	--	1	1	4	5	5	4	2	--	--	81.5
A. nemoptera (Pacific)	17	--	--	--	--	--	--	--	--	--	--	--	2	1	2	5	4	2	--	1	82.1
A. vulpes (Atlantic)	38	1	1	3	6	8	9	3	3	2	2	--	--	--	--	--	--	--	--	--	72.6

Table 6.—*Frequency distribution of scales above and below lateral line, and around caudal peduncle in* Albula nemoptera *and* A. vulpes

Species	Scales above lateral line					Scales below lateral line				Scales around caudal peduncle			
	No.	*8*	*9*	*10*	*Mean*	*6*	*7*	*8*	*Mean*	*16*	*17*	*18*	*Mean*
A. nemoptera (Atlantic)	22	--	18	4	9.2	--	7	15	7.7	19	3	--	16.1
A. nemoptera (Pacific)	19	1	14	4	9.2	--	6	13	7.7	11	7	1	16.5
A. vulpes (Atlantic)	37	5	30	2	8.9	32	5	--	6.1	37	--	--	16.0

Table 7.—*Frequency distribution of predorsal scales in* Albula nemoptera *and* A. vulpes

Species	Predorsal scales												
	No.	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*Mean*
A. nemoptera (Atlantic)	22	---	---	---	1	3	2	7	8	1	---	---	20.0
A. nemoptera (Pacific)	16	---	---	---	---	4	2	4	5	1	---	---	19.8
A. vulpes (Atlantic)	29	2	---	6	8	4	1	1	2	3	1	1	18.1

Table 8.—*Frequency distribution of lower and upper limb gill rakers in* Albula nemoptera *and* A. vulpes

Species	Lower limb							Upper limb							
	No.	*9*	*10*	*11*	*12*	*13*	*Mean*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Mean*
A. nemoptera (Atlantic)	28	6	18	4	--	--	9.9	2	11	6	3	5	1	--	7.0
A. nemoptera (Pacific)	21	--	4	9	8	--	11.2	--	--	--	7	8	5	1	9.0
A. vulpes (Atlantic)	39	--	--	8	27	4	11.9	--	--	10	19	5	3	2	8.2

Table 9. *Frequency distribution of total gill rakers in* Albula nemoptera *and* A. vulpes

Species	Total gill rakers										
	No.	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*Mean*
A. *nemoptera* (Atlantic)	28	4	8	7	4	3	2	--	--	--	17.0
A. *nemoptera* (Pacific)	21		--		1	5	7	6	1	1	20.2
A. *vulpes* (Atlantic)	39	--	--	--	3	9	18	8	2	1	20.0

Table 10. *Frequency distribution of branchiostegal rays in* Albula nemoptera *and* A. vulpes

Species	Branchiostegal rays							
	No.	*10*	*11*	*12*	*13*	*14*	*15*	*Mean*
A. *nemoptera* (Atlantic)	27	--	--	--	14	11	2	13.6
A. *nemoptera* (Pacific)	21	--		--	4	12	5	14.0
A. *vulpes* (Atlantic)	39	7	11	14	6	1	--	11.6

Table 11. *Frequency distribution of vertebrae in* Albula nemoptera *and* A. vulpes

Species	Vertebrae													
	No.	*69*	*70*	*71*	*72*	*73*	*74*	*75*	*76*	*77*	*78*	*79*	*80*	*Mean*
A. *nemoptera* (Atlantic)	20	--	--	--	--	--	--	--	--	3	7	10	--	78.4
A. *nemoptera* (Pacific)	20	--	--	--	--	--	--	--	--	1	9	9	1	78.5
A. *vulpes* (Atlantic)	20	10	10	--	--	--	--	--	--	--	--	--	--	69.5

a comparison of their detailed structures. From the characters studied there is more indication of similarity than divergence. The most important differences between the two species are the larger mouth and the longer last dorsal and anal rays in *A. nemoptera*. Other differences were in dentition, certain proportions, meristic characters, and color markings.

Even their ancestry, as reconstructed from fossil material, indicates that *A. vulpes* and *A. nemoptera* should not be considered as representing separate monotypic genera. Frizzell (1965), after studying otoliths, suggested a phylogeny of albulid genera dating back to the Cretaceous. Although he retained *Albula* and *Dixonina* as separate genera, his illustrations, descriptions, and comments indicate that these two genera are more closely related to each other than either is to any of their predecessors. Both *Albula* and *Dixonina* are tentatively shown by Frizzell to be descended from the Eocene-Oligocene genus *Metalbula* Frizzell.

Radiographs of 20 juvenile to adult *A. vulpes* and 40 juvenile to adult *A. nemoptera* indicate that the otolith (sagitta) of *A. vulpes* is more inclined, with respect to the axis of the vertebral column, than that of *A. nemoptera*. This has been confirmed by Don L. Frizzell (personal correspondence).

ALBULA NEMOPTERA (FOWLER)

Dixonina nemoptera Fowler, 1911; 652 (original description); Santo Domingo, West Indies. Myers, 1936: 83–85 (new record; compared with *Albula;* Acapulco, Mexico). Walford, 1939: 119 (identification of drawing from Kumada and Hiyama, 1937; Gulf of California). Beebe, 1942: 45 (compared with *D. pacifica*). Rivas, 1952: 3 (popular account of new record; Port Antonia, Jamaica). Hildebrand, 1963: 143–145 (description; relationship; range; synonymy; Acapulco, Mexico). Caldwell and Caldwell, 1964: 4 (dorsal fin rays; Jamaica). Berry, 1964: 722 (synonymy with *D. pacifica* questioned). Frizzell, 1965: 85 (otolith-based taxonomy, classification, lineage, paleoecology).

Albula nemoptera Metzelaar, 1919: 9 (description; comments; generic separation not justified; Puerto Cabello, Venezuela).

Albula vulpes (not of Linnaeus) Kumada and Hiyama, 1937: (colored plate; Gulf of California). Caldwell and Caldwell, 1964: 4–5 (dorsal fin rays; tentative identification; Caledonia Bay, Panama).

Dixonina pacifica Beebe, 1942: 43 (original description; compared with *D. nemoptera;* Potrero Grande, Culebra Bay, and Piedra Blanca, Costa Rica). Hildebrand, 1963: 144–145 (synonymized with *D. nemoptera;* Acapulco, Mexico). Berry, 1964: 722 (synonymy with *D. nemoptera* questioned).

A comparison of specimens from the Atlantic and the Pacific Oceans (tables 2 to 11) indicates that *pacifica* should not be considered as specifically distinct from *nemoptera*. No significant differences were found in 18 of the 23 proportional characters studied (table 2). In the five characters that show differences (dorsal and anal fin height, last dorsal ray length, upper and lower caudal lobe length) the overlap is quite broad. Tables 3 to 11 show that meristic characters are about the same in the Atlantic and Pacific populations with the exception of the apparent higher number of gill rakers (tables 8 and 9) in the Pacific population. This exception results from the indistinction of the anterior one or two rakers in the larger specimens because of encroachment by the surrounding spinous areas. The Pacific specimens were smaller than those from the Atlantic by an average of 69 mm.; this is about one-fifth of the largest Atlantic (341 mm.) and the largest Pacific (346 mm.) specimens available. In spite of the apparent difference in the number of gill rakers between the Atlantic and Pacific populations, the overlap is broad and the mean difference small. The Atlantic and Pacific populations do not differ in other characters studied, as discussed below. The number of anal rays (9) not shown in the tables is constant in the Atlantic and Pacific populations.

The Atlantic and Pacific populations of *A. nemoptera* appear to differ slightly in the height of the dorsal and anal fins, the length of the last dorsal ray, the length of the caudal lobes, and the number of gill rakers. These differences, however, do not justify separation at the species level and, probably, not even at the subspecies level. The alleged differences described by Beebe (1942) all break down when adequate material is analyzed.

The following is an itemized description of qualitative characters.

Heart.—The heart of one adult Atlantic specimen was dissected. It has two rows of valves in the conus as in *A. vulpes.*

Gular plate.—Hildebrand (1963: 132), the last reviewer, and most preceding authors, stated that a gular plate is absent in the family Albulidae; however, Nybelin (1960: 78) has demonstrated its presence in *A. vulpes.* Following Nybelin's method (alizarine stain), we found that *A. nemoptera* has a gular plate, similar to that of *A. vulpes.*

Dentition.—A detailed description of Pacific specimens' dentition was given by Beebe (1942). Atlantic specimens are in full agreement with that description. As indicated by Beebe, there is considerable ontogenetic variation in the teeth.

Coloration.—The life colors, based on Pacific specimens, were described by Beebe (1942). Two specimens (UMIM 1028) collected in Port Antonio, Jamaica, were in agreement with Beebe's description. Preserved material has longitudinal dark lines, between the rows of scales, especially above the lateral line. There are an elongate black dash anteriorly on each side of the snout and a median anchor-shaped mark on the tip of the snout extending ventrally towards the mouth.

Size.—The largest known specimen from the Atlantic (Colombia, UMIM 5927) is 341 mm. in standard length, and the largest known Pacific specimen (Acapulco, Mexico, USNM 75547) is 346 mm.

Sex ratio.—The 19 Colombian specimens were sexed: 9 mature males and 10 mature females.

Range.—In the Atlantic the species is now known to occur along the Caribbean coasts of Venezuela, Colombia, and Panama, and at Jamaica and Hispaniola. In the Pacific it is known from Mazatlan and Acapulco, Mexico, and from Costa Rica and Panama.

RELATIONSHIPS WITH *ALBULA VULPES*

A. nemoptera and *A. vulpes* differ in several proportional characters, especially those pertaining to mouth structures and to the elongation of the last dorsal and anal rays into a filament in *A. nemoptera* (table 1). These characters, as well as meristic differences (tables 3 to 11) leave no doubt as to the specific distinction between *A. nemoptera* and *A. vulpes.* As already discussed, however, these are differences of degree not to be considered of generic importance. More basic structural characters such as the presence of a gular plate and two rows of valves in the conus arteriosus are common to both species.

Differences in dentition between *A. nemoptera* and *A. vulpes* are, again, of degree. The premaxillary, dentary and palatine teeth are larger in *A. nemoptera.* Also in *A. nemoptera* the premaxillary band of teeth is two or three teeth wide at the symphysis and three or four in *A. vulpes.* The parasphenoid and entopterygoid teeth, however, are larger and fewer in *A. vulpes.* Maxillary teeth are present in juvenile and young adult *A. nemoptera* to about 250 mm. in standard length, whereas maxillary teeth are present only in juvenile *A. vulpes* less than 50 mm.

The only differences in color pattern between *A. vulpes* and *A. nemoptera* are the markings on the snout. In *A. vulpes* there is a median inverted U-shaped mark on the tip of the snout instead of an anchor-shaped mark and there are no lateral black dashes.

Both species are sympatric, but there is evidence that they may be partially segregated ecologically. This is discussed elsewhere in this study.

For purposes of identification and comparison the most significant differences between *A. nemoptera* and *A. vulpes* are summarized in the following key:

1a.—Vertebrae 77 to 80. Dorsal rays 21, rarely 20. Pelvic rays 9. Pectoral rays 16 to 18, usually 17. Branchiostegal rays 13 or 14, rarely 12 or 15. Lateral line scales 78 to 84, usually 80 to 82. Last ray of dorsal fin prolonged into a filament reaching beyond vertical from tip of pelvic fin (except in specimens smaller than 75 mm. in standard length). Last ray of anal fin prolonged into a filament longer than anal fin base (except in specimens smaller than 75 mm. in standard length). Maxillary reaching beyond vertical from anterior margin of orbit.
.... *Albula nemoptera*

1b.—Vertebrae 69 or 70. Dorsal rays 18 or 19, usually 19. Pelvic rays 10, rarely 9 or 11. Pectoral rays 17 to 19, usually 18. Branchiostegal rays 10 to 14, usually 11 or 12. Lateral line scales 68 to 77, usually 71 to 73. Last ray of dorsal fin not prolonged into a filament reaching beyond vertical from tip of pelvic fin. Last ray of anal fin not prolonged into a filament longer than anal fin base. Maxillary not reaching to vertical from anterior margin of orbit (except in specimens smaller than 70 mm., standard length).
.... *Albula vulpes*

EARLY STAGES OF DEVELOPMENT

Seven larval albulids, collected with four juvenile *A. nemoptera* in Caledonia Bay, Panama (LACM 20467) are tentatively identified as metamorphosing larvae of *A. nemoptera*. This identification was determined by comparing these larvae (table 12) with as many of *A. vulpes* of equal size as could be found in Alexander (1961). To avoid misinterpretations resulting from slight differences in measuring and counting, six larval *A. vulpes* of comparable size from St. Andrews island (UMIM 5928) were included as a control.

The presumed *A. nemoptera* larvae differ from those of *A. vulpes* in predorsal length, preanal length, and number of myomeres (table 12). These differences are confirmed by the comparison of juveniles of *A. vulpes* and *A. nemoptera* (table 13). In both species the number of vertebrae is higher than the observed number of myomeres, and this difference is probably due to the difficulty in discerning the last, very closely approximated myomeres especially in *A. nemoptera*. The apparent greater number of vertebrae in juveniles (table 13) is, on the average, three or four units greater than in adults (table 11) as counted from the radiographs, and this difference may

TABLE 12. *Comparison of metamorphosing larvae of* Albula nemoptera? *and* A. vulpes *of similar size*

[Proportions in thousandths of the standard length]

Character	*A. nemoptera?*		*A. vulpes*			
	Caledonia Bay, Panama, LACM 20467 (7 specimens)		Alexander, 1961: 38–40 (8 specimens)		St. Andrews Island, Colombia, UMIM 5928 (6 specimens)	
	Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*
Standard length (mm.)	58.3–48.8	51.3	57.0–48.5	51.4	56.2–48.0	52.2
Predorsal length	778–815	795	805–830	818	807–825	814
Preanal length	922–971	944	948–980	968	956–975	968
Number of myomeres	69–74	70.8	67–70	67.8	67–69	68.2

TABLE 13. *Comparison of juveniles of* Albula nemoptera *and* A. vulpes *of similar size*

[Proportions in thousandths of the standard length]

Character	*A. nemoptera*		*A. vulpes*	
	Caledonia Bay, Panama, LACM 20467, 20468 (5 specimens)		Guanabo, Cuba, UMIM 758 (5 specimens)	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	36–49	43	30–49	42
Predorsal length	454–467	460	472–490	481
Preanal length	781–793	787	800–817	812
Number of vertebrae	80–81	80.5	72–74	73.0

be explained by the fusion of three or four terminal vertebral centra in adults as pointed out by Hollister (1936).

The presumed leptocephali of *A. nemoptera* are identical to those of *A. vulpes* in general appearance. The juveniles, however, are readily distinguished from those of *A. vulpes* by the much larger mouth. The smallest juvenile *A. nemoptera* (Caledonia Bay, Panama, LACM 20468) was 36 mm. standard length. Four other juveniles from the same general locality (LACM 20467) were 42 to 49 mm.

Alexander (1961) stated that variation in total myomere counts (65 to 72) might indicate subspeciation or even separate species; some of her larvae with 69 or more myomeres may be *A. nemoptera.*

ECOLOGICAL IMPLICATIONS

Frizzell (1965) discussed the ecology and distribution of recent and fossil albulids and suggested that competition between *A. vulpes* and *A. nemoptera* drove the latter to deeper water. This conclusion was based on the study of fossils.

In agreement with the above suggestion all adults (about 200 mm. standard length or larger) of *A. nemoptera* for which capture data are available, were collected in relatively deep water. The 21 *Oregon* specimens (234 to 341 mm.) were collected in trawls in depths of 27 to 110 m. The three Jamaican specimens (197 to 265 mm.) were taken with handline in about 37 m. The Pacific specimens reported by Kumada and Hiyama (1937) were taken by a trawl but no exact depth of capture was given. Of the 19 Pacific specimens reported by Beebe (1942: 44), 5 (220 to 365 mm.) were taken with handline from the ship (*Zaca*) at undetermined depths; the other 14 (80 to 200 mm.) were collected with a seine presumably in shallow water close to the beach.

The senior author has been watching for *A. nemoptera* since 1938, and he has examined hundreds of bonefish in museums and especially in the field throughout southern Florida, the Bahamas, and the Caribbean area. All adult *A. vulpes* came from depths less than 2 m. except one (231 mm., UMIM 5918) taken with three *A. nemoptera* from Jamaica. No specimens of *A. vulpes* were taken with the *Oregon* collections of *A. nemoptera.*

The available evidence suggests that there could be a bathic segregation of adult populations of *A. vulpes* and *A. nemoptera* where the latter occupies the deeper stratum. Overlap in their depth ranges is also suggested, but the depth and width of the overlap zone cannot be determined now.

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RESPONSES OF MARINE ORGANISMS DURING THE SOLAR ECLIPSE OF JULY 1963

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ABSTRACT

Biological and physical observations and measurements were made on the day before and on the day of a total eclipse of the sun, July 19–20, 1963. Totality occurred at 1745 hours (e.d.t.), and observations continued through sunset on both days and in two locations—Bar Harbor and Boothbay Harbor, Maine. Plankton was collected at half-hour intervals, and the activity of herring (*Clupea harengus harengus*) and green crabs (*Carcinus maenas*) was recorded every 15 minutes. Collections of physical data included surface and subsurface illuminance, air and water temperature, salinity, barometric pressure, cloud cover, visibility, and tidal data.

At totality and sunset, the volumes of zooplankton in the surface waters decreased. The responses of copepods varied with the species. *Pseudocalanus minutus* and *Acartia longiremis* showed the most pronounced response and moved towards the surface. Females of *Acartia* were more active than the males. The reactions of other zooplankters were either weak or ill-defined. Herring began schooling near the surface at totality; this behavior, though not as strong, was comparable to that observed at sunset. Green crabs were not active during the eclipse, but were very active after sunset. Similarly, strong echo-tracings were documented after sunset but none were recorded at totality. Apparently the duration of the eclipse was too short or the light intensity too high, or both, to elicit responses from some organisms.

Observations from earlier eclipse studies of marine organisms are discussed and comparisons are made with other field and laboratory studies of behavior in relation to environmental changes.

Animal behavior during solar eclipses has attracted the interest of scientists and naturalists, alike, but relatively few observations of aquatic organisms, particularly marine animals, have been published. A discussion of this lack at a meeting of the Oceanographic Committee of the National Academy of Sciences in 1962 provided the impetus to undertake the observations reported in this paper.

The few specific references to aquatic observations during solar eclipses generally failed to include adequate definition of the physical conditions. Wheeler, MacCoy, Griscom, Allen, and Coolidge (1935) reported on the behavior of fishes and amphibians as observed by game wardens and the interested public during the eclipse of 1932 in the United States. These reports included remarks about feeding habits of freshwater "trout" and "minnows," responses to angling lures, and unusual activity such as pickerel jumping out of the water, and a goldfish eating the tail of another in an aquarium. E. E. Dissell (personal communication, Portland, Maine) reported that a school of pollock (*Pollachius virens*) surfaced during the 1932 eclipse—the earliest observation I located for a marine fish. Some of these reports suggest a suppression of activity at totality and others an increased level of activity; but most of the reports were casual observations by laymen and the significance of the observations is limited.

Probably the first carefully planned series of observations was made by Mori (1939), during the 1936 eclipse in Japan. He studied the responses of insects and birds at totality and mentioned the behavior of the sandhopper, *Orchestia* sp., and the migration of eye pigment in the crayfish, *Cambaroides japonicus.* He also included a brief reference to responses of other crustaceans and several fishes. Weber (1952), though mostly concerned with terrestrial organisms, concentrated his efforts on species whose normal behavior was well known and recorded changes in temperature, light, and

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humidity during a 1952 eclipse in Iraq. Petipa (1955) sampled zooplankton during the 1954 eclipse in the Black Sea, U.S.S.R., and reported that most of these organisms responded by rising towards the surface at totality. K. F. Wiborg (personal communication, Bergen, Norway) made studies off the Norwegian coast during the 1954 eclipse, but poor weather—overcast with strong winds—hampered the collection of zooplankton and interpretation of results. Some of the observations made during the July 1963 eclipse have already been reported. Skud (1964) recorded the responses of herring, *Clupea harengus*, and the green crab, *Carcinus maenas;* and Backus, Clark, and Wing (1965) described changes in depth of the scattering layers and the occurrence of bioluminescent flashes.

Though the number of references dealing with responses of marine organisms to solar eclipses is small, there is a considerable background of information concerning reactions to light—both in nature and in the laboratory. The purposes of this article are to present the more detailed observations made during the eclipse of July 1963, to compare these observations with pertinent information from similar studies, and to add to the general knowledge of phototactic responses and rhythmic behavior patterns.

OBSERVATIONS AND COLLECTING METHODS

The total eclipse of the sun occurred on Saturday, July 20, 1963, and the path of totality bisected the State of Maine (fig. 1). At Bar Harbor, mideclipse occurred at 21:45:00 Ephemeris time (17:44:25 eastern daylight time), the sun's altitude was 25 degrees, the path of totality was 53 miles wide, and the duration was 59 seconds (U.S. Naval Observatory, 1961). All of the State experienced at least 98 percent totality. At totality, cloud cover varied considerably along the coast and obstructed viewing in some areas, as did fog patches in certain offshore areas. At Bar Harbor, the 20-m. Fish and Wildlife Service research vessel *Rorqual* was used as an observation and collecting platform; though a light fog reduced visibility on the water surface to a few miles, the eclipse was fully visible. At Boothbay Harbor, the 14-m. FWS vessel *Phalarope* was used to collect samples. Holding tanks were arranged at the Laboratory dock to study responses of organisms held in captivity. Activity of the captive animals was recorded every 15 minutes. All observations are reported as eastern daylight time unless otherwise specified.

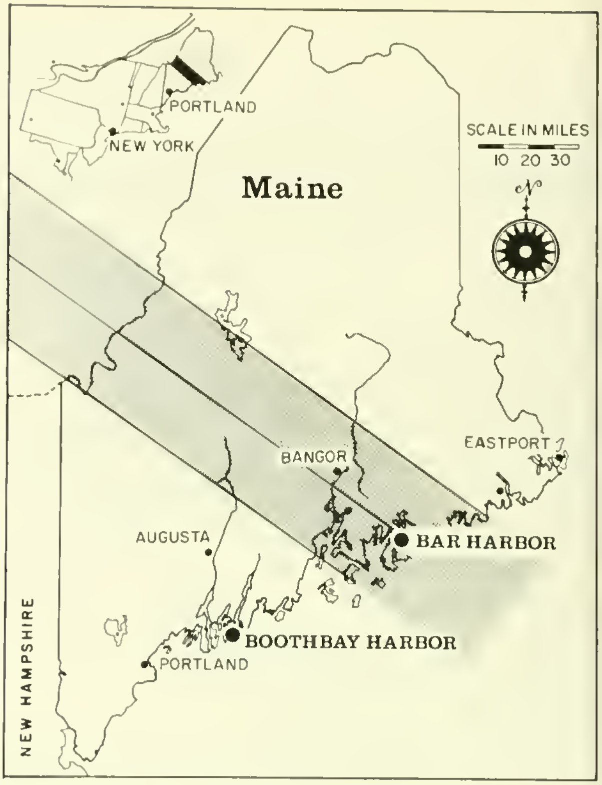

FIGURE 1.—Path of totality and vicinity of sampling areas during solar eclipse of July 20, 1963.

Observations and collections were made on the day previous to the eclipse and on the day of eclipse, beginning at 1600 hours and continuing at intervals through totality (1745) until 2300. The 2-day sequence was intended to provide a test and control in detecting differences in the behavior of animals, as was the extension of observations through sunset and early evening. Light measurements at Boothbay Harbor were made at the surface with a Gossen Lunasix electronic exposure meter.[1] This meter lacked the flat interception screen necessary for precise measurement of illumination, but the incident light readings did provide an index for comparing the illumination between and within days. Aboard the *Rorqual* an irradiance meter (Model C-1a, Marine Advisors, Inc.) equipped with Weston photronic cells measured subsurface changes in light penetration. This unit had a filter with a peak sensitivity of 550 millimicrons and a range of 390 to 760 millimicrons. The irradiance meter provided the ratio of the amount of radiation at the depth of the submerged cell to a reference cell on deck. Secchi-disk readings also were taken at regular intervals. Plankton samples were taken at half-hourly intervals with Miller high-speed samplers at Bar Harbor, and at hourly intervals with the Clarke-Bumpus sampler at Boothbay Harbor. Temperature and salinity were recorded and echo soundings were made continuously during the sampling period.

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[1] Trade names referred to in this publication do not imply endorsement of the products.

PHYSICAL CHANGES

Measurements at Boothbay Harbor showed that illuminances on the day before the eclipse were (control day) and the day of the eclipse was not closely comparable (table 1). Except for the period of totality, surface illumination was far greater on the day of the eclipse than on the control day. This difference was also evident from other data. Visibility on July 19 was limited to 9 km., and nine-tenths of the sky was covered by cirrostratus clouds; on July 20, objects were visible at 16 km. and the stratus cloud cover of seven-tenths was generally dissolving. These differences limited the comparisons which could be made between test and control days.

The decrease in surface illuminance before and at totality and the subsequent increase are documented in table 1. An hour before totality, 75,000 luxes were recorded, 900 at totality, and 28,000 within the hour after totality. Darkness at totality (1745) approximated that which occurred one-half hour before sunset. Though the primary purpose of Secchi-disk observations was to measure water clarity, the results also provided information on the submarine light penetration during the eclipse. The extinction depth of the Secchi-disk was 7.0 m. at 1600,

TABLE 1.—*Surface illuminance at Boothbay Harbor, July 19 and 20, 1963*

Time (e.d.t.)	July 19	July 20
	Luxes	*Luxes*
1546-1600	38,000	>100,000
1601-1615	38,000	>100,000
1616-1630	33,000	>100,000
1631-1645	75,000	75,000
1646-1700	93,000	------------
1701-1715	64,000	75,000
1716-1730	------------	55,000
1731-1745	24,000	[1] 900
1746-1800	24,000	1,050
1801-1815	11,500	24,000
1816-1830	9,500	28,000
1831-1845	16,750	19,000
1846-1900	4,800	16,600
1901-1915	3,600	16,600
1916-1930	3,600	3,600
1931-1945	900	825
1946-2000	265	[2] 265
2001-2015	110	------------
2016-2030	20	50
2031-2045	<10	<10
2046-2100	<10	<10

[1] Totality.
[2] Sunset.

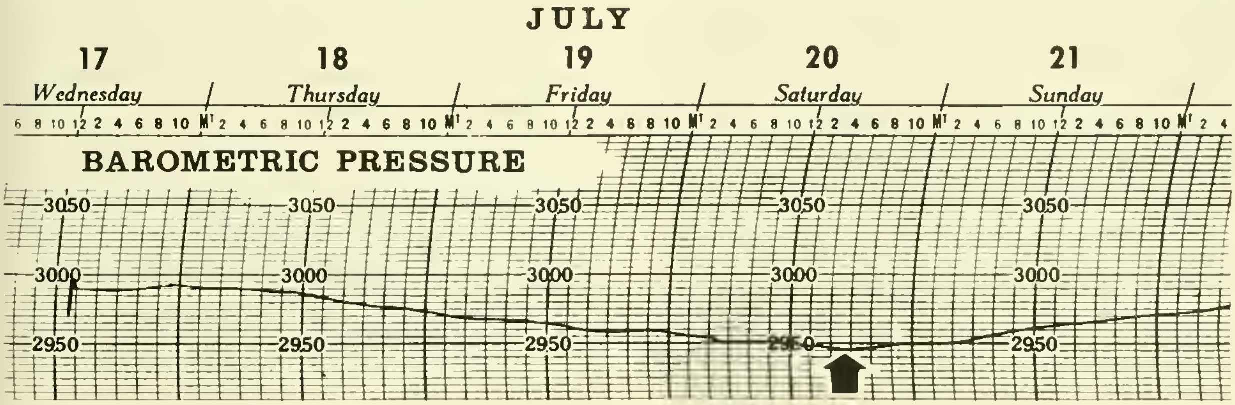

FIGURE 2.—Barometric pressure, mm. of mercury, adjusted to sea level, at Boothbay Harbor. The arrow indicates time of totality.

5.5 m. at totality, 6.0 m. at 1 hour after totality, and 5.5 m. at sunset.

In conjunction with these observations, barometric pressure was measured from Wednesday, July 17 through Sunday, July 21 (fig. 2). Totality coincided with the low pressure reading (29.45 mm.) for the period of observation. The consistent decline in pressure before the eclipse and the rise after totality may or may not be coincidental, but I have been unable to locate similar records from other eclipses.

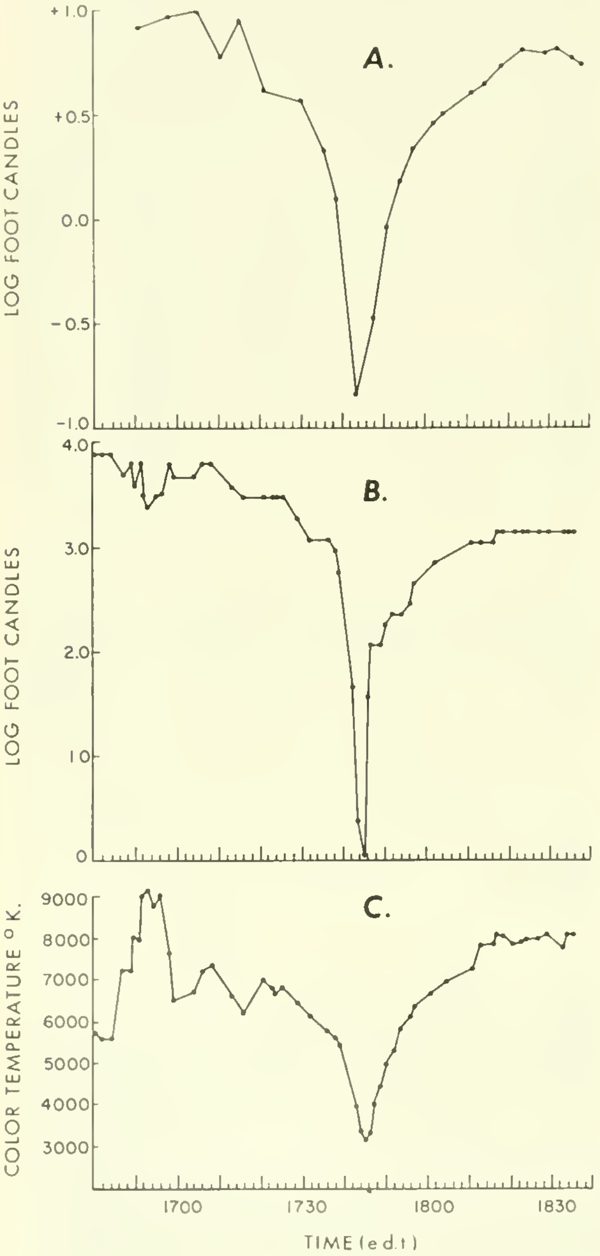

FIGURE 3.—Time-light curve from: A. photometer; B. Gossen light meter; and C. Gossen Sixticolor meter. (One foot-candle = 10.76 luxes.)

Observations aboard the *Rorqual* in Bar Harbor were supplemented by land-based observations on Mount Cadillac. LFE Electronics (Boston) conducted a series of tests and supplied me with comparative measurements of a time-light series (fig. 3). The differences among the curves are largely due to the different spectral responses of the photo cells and filters. This information provided an independent comparison of our own measurements with the irradiance meter (table 2). Ten minutes before totality, the illumination at the surface registered 4,000 luxes, the lowest value in the series of measurements before and after totality. Subsurface values were also lowest at this time. As is evident from these data, the eclipse occurred during a normal period of declining brightness, but the substantial reduction in illumination at or near totality and the subsequent increase clearly distinguishes the influence of the eclipse. During the eclipse, air temperature declined from 15.3° to 12.5° C., and water temperature at the surface declined from 12.8° to 11.3° C. Though the eclipse may have accentuated the temperature change, the late afternoon decline was anticipated. Water temperature at depth remained nearly constant; 1 hour before totality it was 10.3° C. at 10 meters; 9.3° at 20 m.; 8.3° at 30 m.; and 7.8° at 60 m. Salinity ranged from 31.35 to 31.74 ‰ at the surface and from 32.09 to 32.23 at 60 m. These differences in salinity were assumed to be caused by tidal

TABLE 2.—*Surface and submarine illuminance (luxes) during the eclipse at Bar Harbor, Maine*

Depth	Time (e.d.t.)				
	1612	1657	1735[1]	1804	1840
Meters	*Luxes*	*Luxes*	*Luxes*	*Luxes*	*Luxes*
Surface	36,000	27,800	4,000	4,800	6,200
5	7,600	5,800	800	1,100	1,500
10	2,600	1,500	400	700	500
15	1,100	700	100	200	150
18	500	300	0	100	100

[1] Totality 1745 e.d.t.

movements. Low tide was at 1646 hours and was -0.08 m.; high tide occurred at 2256, and was 4 m. A light fog sometimes hampered vertical visibility but generally did not obscure the sun.

BEHAVIOR OF ZOOPLANKTON

Cladocerans and copepods were the most numerous zooplankton, accounting for more than 90 percent of the plankters. Less abundant groups included gastropods, brachyurans, and decapod larvae, cirriped nauplii, and chaetognaths. Total volumes of zooplankton and the distribution of seven species of copepods were examined to determine any behavioral changes during the eclipse.

Though the light intensity on July 19 was lower and more variable than on the day of the eclipse, this difference did not totally negate the comparison of zooplankton distribution on the test and control days. Miller high-speed samplers (without meters) were used at Bar Harbor; and Clarke-Bumpus samplers (with meters) at Boothbay Harbor. The zooplankton volumes from surface tows in the two locations are compared in figure 4, along with the changes in light intensity during the 2 days. Although this comparison does not account for amounts of water strained for either gear, the duration of tows in each locale were nearly the same, and the changes in zooplankton abundance which were recorded for the different gears followed similar trends. On both days, the surface volumes of zooplankton decreased at or near sunset and then increased rapidly during the following hour. On the day of the eclipse, a similar decrease was noted at totality, both at Bar Harbor and Boothbay Harbor. This phenomenon was also evident in the quantitative data from the Clarke-Bumpus samplers. Volumes of collections made at the surface were 130 cc./10m.^{3} an hour before the eclipse, 67 cc./10m.^{3} at totality, and 105 cc./10m.^{3} an hour after totality. The decrease in volume also was noted at 20 m.—231 cc./10m.^{3} an hour before totality, 165 cc./10m.^{3} at totality, and 222 cc./10m.^{3} an hour later. At intermediate depths, 3 to 10 m., there was no pronounced change in volume at totality.

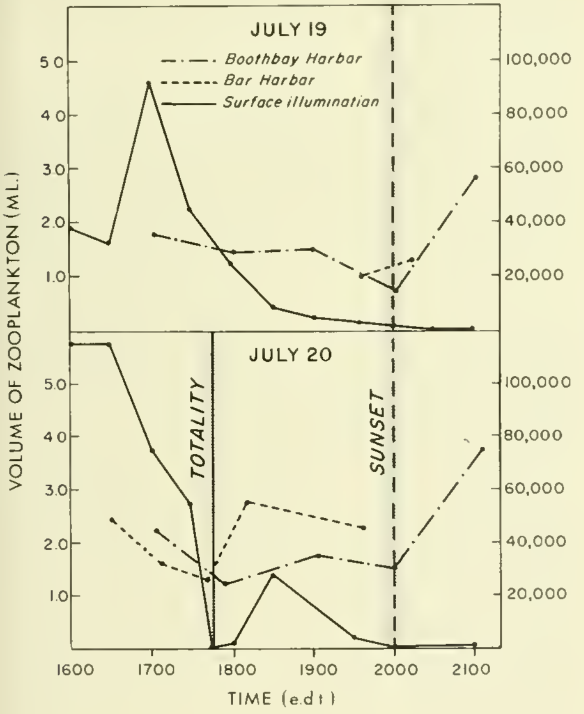

FIGURE 4.—Surface volumes of zooplankton from two sampling locations compared with surface illumination at Boothbay Harbor.

The distribution of seven species of copepods differed measurably on both the test and control days and during the period of the eclipse. On July 19, *Pseudocalanus minutus* and *Acartia longiremis* occupied shallower strata of water than on July 20, which was the brighter day. These species also showed the most pronounced response during the eclipse. The upward movement of these two species and the differences in vertical distribution between days are shown in figure 5. The responses of *Centropages hamatus, Tortanus discaudatus, Calanus finmarchicus, Temora longicornis,* and *Eurytemora herdmani* were not as well defined as those of *P. minutus* and *A. longiremis*, and the responses of some species differed at the two sampling locations. For example, the numbers of *C. finmarchicus* and *T. longicornis* from the surface to 10 m. increased during the eclipse at Boothbay Harbor, but declined at Bar Harbor. The abundance of *E. herdmani* was so limited in Bar Harbor that its distribution could not be plotted reliably; in Boothbay Harbor this species was one of the most abundant

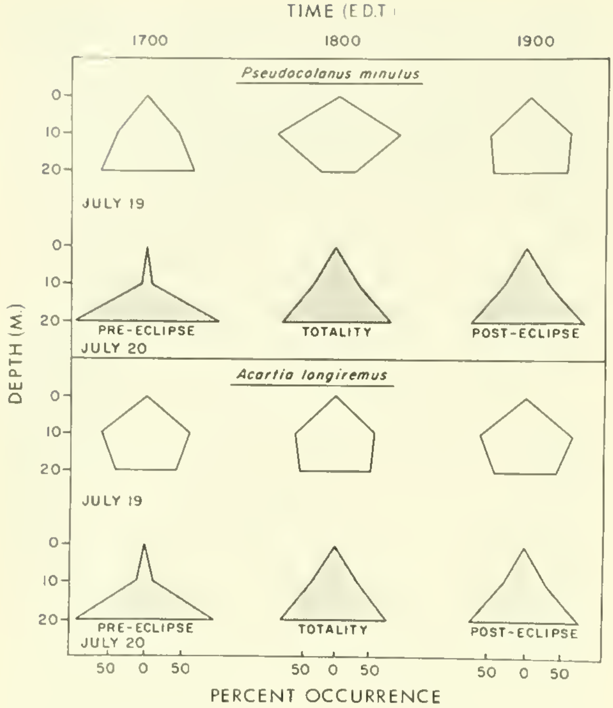

FIGURE 5.—Depth distribution of two species of copepods before, during, and after the eclipse.

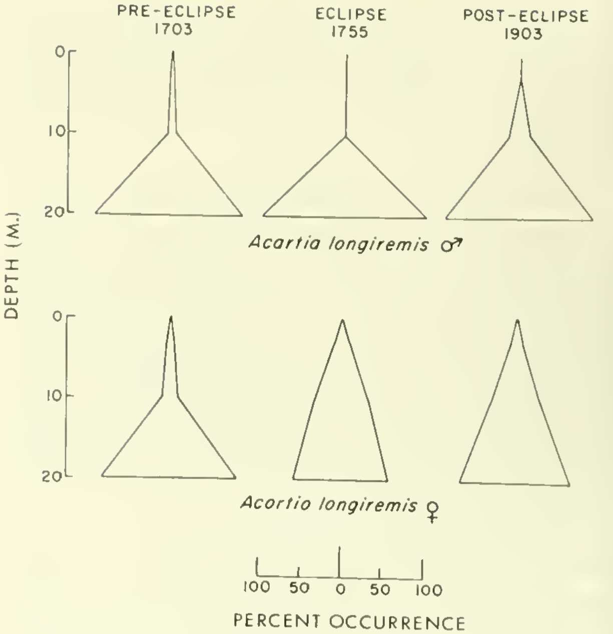

FIGURE 6.—Depth distribution in percent of male and female *Acartia longiremis* during the eclipse.

forms, but showed no appreciable change in distribution during the eclipse. Though more frequent sampling might have established a basis for understanding these differences, it is evident that all species did not respond in the same degree or in the same manner.

The lack of uniformity among species and within species was not peculiar to the eclipse study. Wynne-Edwards (1962) summarized several early works which demonstrated the differences in behavior of copepods. Clark (1933 and 1934) discussed diurnal changes in vertical distribution relative to sex and age-groups and reported the stronger migratory habits of adult female *C. finmarchicus*, which rose much nearer to the surface at night than did the male. During the eclipse, female *A. longiremus* were more active than males and were more prevalent at the surface (fig. 6). There was a suggestion of a reversal of this phenomenon in *P. minutus*, and no difference in the distribution of sexes in *T. longicornis*. During the eclipse of 1954, Petipa (1955) reported that vertical migration in the Copepoda was restricted almost entirely to adult females. In all of his samples, females of *A. clausi* were concentrated in the upper layers and the males at lower depths.

BEHAVIOR OF THE GREEN CRAB

Naylor (1958) observed that the rhythmic activity of green crabs (*Carcinus maenas*) could be divided into two components, one of diurnal frequency with a peak at night, and the other, a tidal frequency with a peak at high tide. On the day of the eclipse, low tide occurred an hour before totality and high tide three hours after sunset; consequently the behavior of the crabs could be judged independently of their response to tides.

Thirty crabs, 15 of each sex, were used as test animals. The mean width was 62 mm. (range, 42–79 mm.) for the males, and 60 mm. (range, 51–69 mm.) for the females. The males were banded so that the sexes could be readily distinguished during the experiment. The crabs were placed in a fiberglass tank 1.3 by 1.0 by 0.5 m. that had a 7-cm. layer of sand and gravel on the bottom (fig. 7). One corner of the tank was covered with fiberboard to provide a darkened shelter. Running water

FIGURE 7.—Fiberglass tank for holding green crabs.

was supplied from the laboratory salt-water system and the tank was placed out-of-doors in an area free from shadows. Naylor (1958) found that the normal precision and level of the rhythmic activity declined after the crabs had been held for 3 to 4 days. For my study the crabs were placed in the tank two days before the eclipse and took refuge in the shelter immediately. Activity was recorded by counting the crabs that left this cover. A control was established by making observations periodically during the day before the eclipse and at 15-minute intervals from 1600 to 2200 hours, well past sunset.

On July 19 no crabs left the sheltered area until 2035. From that time until the last observation at 2205 the activity generally increased; as many as 11 males and 10 females left the covered area; the average number of active males was 5.7 and the average number of females 5.2. On the day of the eclipse, July 20, no activity was observed until 2050, more than 3 hours after totality; the greatest number of males in the unsheltered area at any time was 13, and the highest number of females 5; between 2050 and 2200 the average number of active males was 9.2 and females, 3.6.

Because the crabs were not active during the eclipse, other experiments were conducted the following day to determine light conditions which would elicit a response. When the tank was in daylight (27,000 luxes) and then covered by a heavy tarpaulin that reduced the light to less than 10 luxes, 2 minutes elapsed before any activity was noted. Under conditions of subdued artificial light of 500 luxes, which was then reduced to less than 10 luxes, the response was more rapid; 3 crabs were active within 30 seconds and as many as 10 came out of the shelter within 2 minutes. As in the observations made on the date of the eclipse, the males were the first to respond. The light intensity in the half hour before totality was considerably greater than that of the artificial light; apparently the duration of subdued light during the eclipse was too short or the intensity too high to elicit a response from the crabs.

BEHAVIOR OF HERRING

Generally, the behavior of Atlantic herring *(Clupea harengus harengus)* is well documented, but specific responses are extremely variable. Blaxter and Parrish (1965), studying vertical movement, concluded that it was not possible to show any relationship between the preferred depth, or the extent of upward movement, and such factors as gradients of salinity, temperature, or food. The herring used in the eclipse study had been held in large tanks for several weeks. Though their behavior could not be considered comparable to that of herring in their natural environment, the fish were acclimated to confined conditions which were necessary for the observations made during the eclipse.

About 75 two-year-old herring were placed in a small-meshed holding pen during early morning of July 19. Observations were made at 15-minute intervals from 1600 to 2200 hours on July 19 and 20. The pen (dimensions, 3 by 3 by 2 m.) was visually separated into quadrants A, B, C, and D (fig. 8). Each quadrant was divided into two sections by an imaginary plane midway between the surface and the bottom of the pen. The presence or absence of fish in these quadrants and the depth divisions were recorded, along with remarks on schooling and directional movement. On both days, there

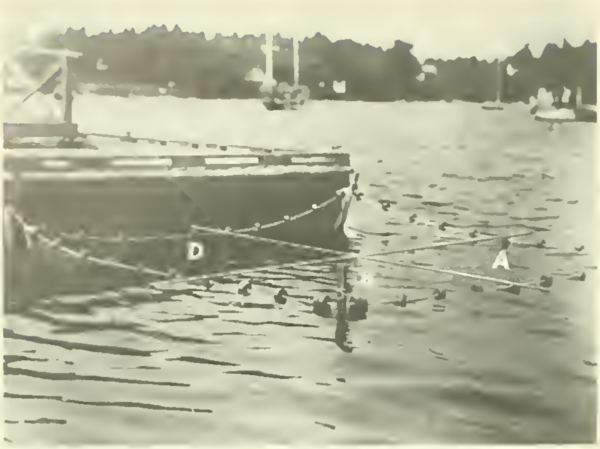

FIGURE 8.—Impoundment for herring, showing quadrants used to record observations.

was only one period (30 to 45 minutes) during which no fish were in the upper layer; this distribution occurred about an hour before sunset (2000). Similarly, there was only one period during which no fish were located in the lower layer. This period began one-half hour after sunset and continued for 45 to 60 minutes, after which herring were dispersed throughout the holding pen.

During daylight herring were more numerous in the upper area of quadrants A and B than in C and D. This difference probably is explained by the uneven distribution of light. Quadrants C and D were located closest to the vessel float which was used to anchor the holding net. The upper areas of these quadrants were shaded by the float and were avoided by the fish. The distribution of herring in the lower layers of A-B and C-D was relatively uniform. After dark, fish were equally dispersed in the upper and lower layers of the pen.

On the day of the eclipse, fish were distributed in the upper layers of quadrants A and B and in the lower layers of quadrants A, B, C, and D. Fish were absent from the upper layer of quadrant D until sunset. No fish were observed in the upper layer of quadrant C from the start of observations at 1600 until 1730—15 minutes before totality. Fish were active in this quadrant from 1730 until 1800; were absent at 1815; and reappeared from 1830 to 1900. This movement of fish into quadrant C at the approach of totality was coupled with a change in behavior of herring in the other quadrants. Some fish began to school and moved to the surface of the water. This was in contrast to the preeclipse behavior of general dispersion without movement at the surface, and apparently was in response to the reduced light during the eclipse. The response was not strong, and not all fish reacted to the change. The data on subsurface illumination (mentioned above) suggests that the duration of lowered light intensity at totality was not enough to stimulate a stronger response. This conclusion is supported by the observations at sunset, when the decrease in light approximated that of the eclipse, but for a longer period, and elicited a stronger schooling response from the herring.

ECHO SOUNDINGS

Echo sounders aboard the two vessels were run continuously during the study, but none of the records showed any change or movement of organisms during the eclipse. Echo tracings in Boothbay Harbor documented considerable activity in the early evening on July 19 and 20 (fig. 9). On July 19, activity was first detected at 1854 when minor peaks and streaks extended up from the bottom. By 1955, some of these streaks and dots were no longer in contact with the bottom; others remained in contact but were extended and more pronounced. By 2100, only a few of these marks were in contact with the bottom; the rest were scattered from the bottom to the surface. This phenomenon was also recorded on the evening of July 20, though somewhat later and less pronounced than on the previous evening.

None of the organisms taken in the plankton nets was large enough to account for the markings observed on the recording paper, and the scheduled collections did not allow time to utilize other gear on July 19 or 20. On July 21, a trawl was fished during late evening in the same area. Echo soundings were similar to those on July 19 and 20. Large catches of jellyfish *(Aurelia aurita)* were taken in the net; presumably they were the animals detected by the sounder, but the possibility exists that the tracings were from herring or other fish that escaped capture. In any case, the lack of response from these organisms during the eclipse indicated that the lowered light intensity or duration of totality, or both, were not sufficient to stimulate the kind of movement observed after dark.

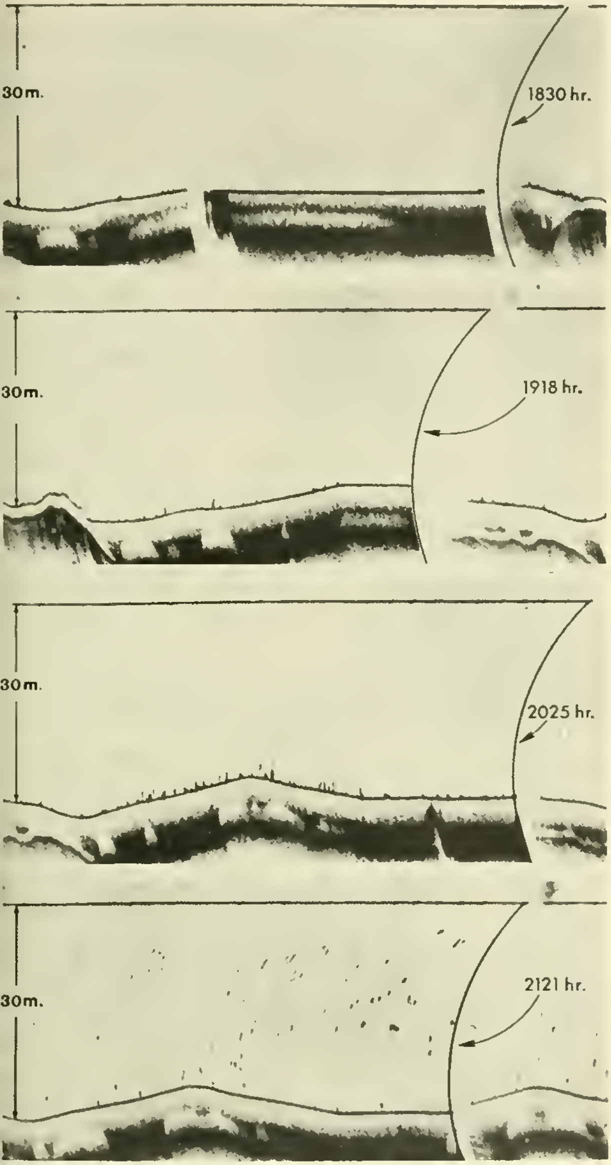

FIGURE 9.—Echo soundings before and after sunset (2000 hr.).

COMPARISON WITH OBSERVATIONS FROM OTHER ECLIPSES

The observations presented in this paper show some agreement with those of previous workers, but the responses recorded for some species were not the same. Considering the variables such as light intensity, duration of totality, and the variation in experimental design, these differences are not surprising, but they should be equated.

Mori (1939) conducted carefully designed experiments on several species, and made detailed observation on others, including the sandhopper, *Orchestia* sp. He concluded that sandhoppers "were apparently not affected by the eclipse," yet he does mention that a few individuals were exposed "towards the end of totality . . . . ," exhibiting their normal crepuscular behavior, but this activity lasted only a few seconds before the animals retreated into hiding. Totality during the 1936 eclipse in Japan lasted 2 minutes, and began at 1519 when illuminance under normal conditions is high. As Mori stated, the inactivity may be explained by the fact that the change of light intensity at totality was too rapid; but he also cautioned that factors such as humidity and atmospheric pressure might have been the controlling influences. He also reported on observations from the aquarium of the Akkesi Marine Biological Laboratory, ". . . shrimp, a flat fish, a young salmon, a trout, and a herring were all indifferent to the eclipse, whereas a crab, which is quiet on ordinary days, began to move, and a bullhead appeared from the shady tangle of weeds when it became darker and hid again when it became lighter in just the same way as seen on ordinary days and nights."

In reference to light-dark cycles, Bünning (1964) stated that deviations from the natural frequency of an organism could "necessarily have an entirely different relationship to the light and dark period than normally. For example, if the dark period is too short, the organism with its own cycle length does not have time enough within the dark period to reach the usual physiological state typical of night." He also stressed that sometimes the beginning of the light period has a greater influence on the timing of responses during dark than the beginning of the dark period itself.

Other factors could also contribute to the degree of response. Of particular interest is the barometric pressure. As shown in figure 2, the pressure declined continuously for the 2 days preceding the 1963 eclipse. Brown (1958) showed that cycles of activity in certain organisms fluctuate with changes in pressure. These species included the fiddler crab (*Uca*), the oyster (*Ostrea*), and the quahog (*Venus*). Though these animals also exhibit daily and lunar cycles of activity, mean hourly rates of activity were correlated with the rates of rise or fall in barometric pressure. Activity increased with the hourly rate of fall and decreased with the rate of rise. The importance of this phenomenon to the observations during the 1963 eclipse is uncertain; it could be of significance during an eclipse with a relatively long period of totality.

In comparing the responses of zooplankton during the eclipses of 1954 and 1963, the importance of documenting the environmental differences is readily apparent. Petipa (1955) reported that most species reacted by rising to the upper water layer (0-5 m.) during the eclipse and by descending to lower depths (5-14 m.) after the eclipse. The strongest response was from *Sagitta*, and larvae of Decapoda, Lamellibranchia, and Gastropoda. His work was done in the Black Sea at Sevastopol Bay where surface temperatures during the eclipse (June) were at least 20° C. Zenkevitch (1963) described the general hydrological features of the Black Sea: salinity varied between 17 and 18 ‰ at the surface and was only 22 to 23 ‰ in deep water; temperature at 25 m. was 14° C. in summer and 6° C. in winter; dissolved oxygen content ranged from 1.05 to 7.76 cm.^{3}/l. at 50 m. and declined rapidly with increasing depth below 50 m.; water deeper than 150 m. was contaminated with hydrogen sulphide; Secchi disks disappeared between 18 and 21 m.; and most species of zooplankton were found at depths above 50 m. and were concentrated between the surface and 25 m. Many of these characteristics are strikingly different from those in the coastal waters of the Gulf of Maine: during the eclipse of July 20 the temperature was less than 15° C. at the surface and was 10° C. at 10 m.; salinity was about 32 ‰; and the Secchi disk disappeared at less than 10 m. The dissolved oxygen content in the Gulf of Maine was reported by Gran and Braarud (1935) to vary between 5.5 and 7.8 cm.^{3}/l. at 40 m., and Bigelow (1926), in contrast to the conditions in the Black Sea, reported many species of zooplankton below 50 m., some of which had their densest concentrations below 100 m.

Other differences to consider include the characteristics of the eclipse and the location of sampling in relation to the path of totality. The sampling sites in Maine were selected because they lay in or near the path of totality. In contrast, Sevastopol Bay was about 400 miles from the path of totality in 1954. (This figure was estimated from eclipse data presented by Oppolzer, 1962.) As Petipa (1955) did not provide any measure of light intensity, one can only assume, other things being equal, that the illuminance during the eclipse was higher at Sevastopol than at Bar Harbor. Yet Petipa recorded more activity of zooplankton than was noted in the Gulf of Maine. Differences in species were important, but I suspect that the differences in the two environments were more critical.

Though not a species encountered in this study, experimentation on *Daphnia* offers several plausible explanations for the zooplankton behavior observed during the eclipse. Harris and Wolfe (1955) found that *Daphnia* responded rapidly to changes in light intensity, moving in the direction of the original optimum intensity, but this was followed by movement towards an adapted optimum and resulted in little change of position. In essence, a high change of intensity produced an alteration of photonegative and photopositive phases, and the net result had relatively little effect on the depth at which the animal was located. When changes in light intensity were slow, however, the animals simply followed the movement of the original optimum zone. Ringelberg (1964) disagreed with the explanation of the phototactic response offered by earlier workers; he concluded, on the basis of a very thorough laboratory and field study, "that the directing stimulus for the phototactic reaction is a contrast or a gradient present in the angular light distribution." Schallek (1943) reported that *Acartia tonsa* in a glass cylinder would move upwards when illuminated from above and downward when illuminated obliquely. He considered the reaction of *A. tonsa* to diffuse light in the cylinder to be in accord with the downward movement in the ocean during the day, but that the reaction to direct light under experimental conditions had no bearing on its behavior in nature.

These experiments emphasize the importance of other variables that one must consider in attempting to compare and evaluate observations during an eclipse. The time of day and resultant attitude of the sun in relation to water clarity are of particular concern. Holmes (1957) discussed the penetration of water by light and explained that "The extinction of daylight in the sea is caused by absorption (by the water itself, by particles, and by dissolved substances) and by scattering (by the water and by particles)." Ringelberg (1964) and Schwassman and Hasler (1964) have recognized the importance of absorption and scattering on the phototactic behavior of aquatic organisms; the former paper referred to *Daphnia,* especially the orientation of the eye axis and the body axis, and the latter referred to sun orientation of fishes.

The responses of herring observed during the 1963 eclipse were in general agreement with reports of other observations under varying conditions of light intensity. Johnson (1939) studied captive herring in southern New Brunswick and concluded that, in the absence of direct sunlight, these fish "extended to the surface at all times—dawn, sunrise, cloudy days, sunset, dusk, moonlight, starlight, and cloudy nights." He also found that during daylight, the depth of the fish was greatest when the sun's altitude was highest and the largest fish were in the deepest water. Blaxter and Holliday (1963) summarized the work of European scientists, particularly in the North Sea where the diurnal migration pattern of herring is well documented; and the depth of herring shoals has been correlated with isolux lines to estimate the optimum depth for setting gill nets.

In studying diurnal changes in behavior of adult herring, Blaxter and Parrish (1965) found that the depth (and light intensity) at which the fish occurred during the day was extremely variable; and demonstrated that fish did not move towards the surface until illuminance decreased to 10 luxes. These authors also reported that "recruit fish (2½–3 years old)" remained in higher light intensities by day. The eclipse study lends support to this latter conclusion. Though the response of 2-year-old herring at totality and at sunset was limited, the light intensity was above the level that Blaxter and Parrish observed as necessary to elicit a surface movement by adults. Breder (1951 and 1959) discussed the influence of light on the social grouping of many species of fish and provided a thorough summary of other scientists' work in this field. He stressed the differences in responses by individuals, by sex, and by species. This emphasizes the need to select species whose behavior patterns are well known, when attempting to evaluate the effects of a solar eclipse. The Atlantic herring, in this regard, is a suitable species, except that the sexes cannot be distinguished readily through external examination.

Mention should be made of the types of periodic activity and their importance to the observations made during the eclipse. Allee, Emerson, Park, Park, and Schmidt (1949) classified successive diel periods into two types: exogenous, "in which the pattern is directly induced and controlled by periodic environmental influences" and endogenous, "in which the pattern is resident in the organism." Aschoff (1960) elaborated on the definitions, explaining that an environmentally controlled periodicity (exogenous) will cease under artificially constant conditions; whereas, periodic factors of the environment only serve as synchronizing agents (Zeitgeber) for circadian or endogenous periodicity. He pointed out that a single environmental event can never synchronize continuously and therefore cannot operate as a Zeitgeber. This implies that observations made during an eclipse should not, of themselves, be used to determine whether a response or lack thereof is indicative of either an exogenous or endogenous rhythm. On the other hand, these observations can provide supporting evidence for laboratory or other field experiments concerned with rhythmic behavior patterns. Cloudsley-Thompson (1961) cautioned that rhythmical activities of an animal are not necessarily all of one type and stated that rhythms solely dependent on the environment are rare and probably represent rhythms which are independent but out of phase with the environment. In regard to field observations during solar eclipses, he concluded that the results agree with those of laboratory experiments, in that certain animals exhibit some periodic activities that appear to be dependent on the environment and others that are more markedly independent.

SUMMARY

1. A total eclipse of the sun occurred in Maine on July 20, 1963. Totality lasted 59 seconds.

2. Biological and physical observations were made on the day before the eclipse and the day of the eclipse and were continued through sunset each day to provide a comparison with regular light-dark cycles.

3. Surface and subsurface illuminance declined markedly at totality, approximating conditions at sunset.

4. Barometric pressure declined steadily for the 2 days prior to the eclipse, reached a low point 29.45 mm. at totality, and then increased.

5. Zooplankton volumes from surface waters decreased during the eclipse and at sunset at both of the sampling areas.

6. Of the dominant copepods, *Pseudocalanus minutus* and *Acartia longiremis* exhibited the most pronounced response to the eclipse and moved toward the surface. The reactions of other species were either weak or ill-defined.

7. Female *Acartia longiremis* were more active than males during the eclipse, and moved toward the surface at totality.

8. No change was observed in the behavior of green crabs during the eclipse. Apparently, the duration of the eclipse was too short or the light intensity too high, or both, to elicit a response.

9. At totality, Atlantic herring held in a pen responded in a manner comparable to that observed at sunset. The response was not strong, but some fish began schooling and moved into the surface waters.

10. Echo tracings documented a movement toward the surface after sunset, but tracings during the eclipse showed none of this activity. Though large catches of jellyfish were taken, the traces could have been made by fishes which escaped the net.

11. Comparisons of my observations with those made during other eclipses emphasize the importance of designing experiments carefully to assess properly the behavioral responses in relation to environmental changes.

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SHELL DEFORMITY OF MOLLUSKS ATTRIBUTABLE TO THE HYDROID, *HYDRACTINIA ECHINATA*

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ABSTRACT

The colonial hydroid, a common epizoon on the external surface of the shell of the sea scallop, *Placopecten magellanicus,* sometimes becomes established on the internal shell surface. This intrusion interferes with the normal activities of the scallop's mantle, often causing shell deformity. The scallop reacts by producing a new shell edge within the existing perimeter of the shell and bypassing the hydroid colony. This relation is amensal—one organism is inhibited, and the other is not affected. No proof was found that the hydroid may ultimately cause the death of the scallop.

These same hydroids, in symbiotic association with pagurid crabs, deform and enlarge the apertures of empty gastropod shells. Enlargement of the "house" is to their mutual advantage.

The availability of surface on which to attach and grow is vital for sessile fouling organisms. The larval forms of these species must eventually settle on firm substrate or perish. The organisms are often able to augment available substrate by settling on the surface of other organisms. The upper valve of the sea scallop, *Placopecten magellanicus* (Gmelin), provides such a surface.

Organisms found on shells of sea scallops are those which are found on any suitable substrate in the vicinity. They are commensals, typical epizoa competing for space. They may be pelagic and settle by chance in a particular area, or benthic and possess mobility during larval and early postlarval stages.

Postlarval commensal species found on the sea scallop include representatives of most marine phyla (Merrill, 1961). Most abundant are the boring sponges, sea anemones, branching and encrusting hydroids and bryozoans, pelecypods, barnacles, tubeworms, and simple and colonial ascidians. Wells and Wells (1964), reporting on a calico scallop, *Aequipecten gibbus* (Linnaeus), community study, made similar observations. They found that of the major taxonomic groups only Asteroidea and Ophinoidea were lacking on calico shells.

Most of these animals have a casual association with the sea scallop. They may gain to some extent in having a shell substrate on which to live and possibly by having particles of food brought to them by water currents produced by the scallop. Although the commensal may cause little inconvenience to the host, the scallop certainly does not appear to benefit from the association. In fact, the association may be detrimental to the scallop if extensive fouling of the shell hinders swimming, or if marine borers excavate excessive quantities of the shell; but usually the association provides neither advantage nor harm to the participants.

An association in which the sea scallop is placed at a distinct disadvantage was observed during routine sea scallop studies. The colonial hydroid, *Hydractinia echinata* (Fleming), which grows frequently on the external shell surface of the sea scallop, was observed occasionally to expand around the shell periphery and invade the internal shell surface. The forward elements of the colony, coming in contact with the mantle of the scallop, caused certain inhibitory reactions by the scallop. This paper describes the association, emphasizing the means by which the scallop reacts to internal

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shell invasion. This type of relation in which one of the associates is inhibited while the other is not affected is best described by the term amensal as defined by Odum (1953).

BRIEF REVIEW OF THE LIFE HISTORY OF *HYDRACTINIA ECHINATA*

Hydractinia echinata is far less exclusive in its choice of habitat than earlier observers indicated. It has been dredged "on every sort of bottom" (Sumner, Osburn, and Cole, 1913), and has been found on a wide variety of substrate (Hargitt, 1908). Bunting (1894) mentioned that the hydroid lives on the sea mussel, *Mytilus edulis* (Linnaeus), and Moore (1937) recorded its occurrence on the shell of another bivalve, *Pectunculus* (=*Glycymeris*), but I have seen no other reports of the association of this hydroid with a specific bivalve.

Hydractinia echinata is the well-known hydroid which served formerly as the classic example of symbiosis with the hermit crab, *Pagurus bernhardus* (Linnaeus). Many papers have dwelt on the symbiosis of pagurids and actinians (see Balss, 1924, and Dales, 1957 for a summary of the literature). From experimental studies, however, Schijfsma (1935) concluded that the association of *H. echinata* and *P. bernhardus* could not be defined as true symbiosis—that the hydroid is merely an epizoon.

Schijfsma (1939) described the early stages of growth of colonies of the hydroids, and Fraser (1944) and others have reported in detail the specialization of individuals that make up a colony of *Hydractinia echinata*. This hydroid is polymorphic. Several types of zooids develop, including special generative zooids that produce male and female sporosacs. The ova are fertilized in situ, and after being discharged sink to the bottom where they develop into mobile planulae in 24 to 48 hours. The planulae are never free-swimming; rather they crawl or glide in the manner of turbellarians. The mobile phase lasts at least 24 hours, ending when the planulae fix themselves to a substrate and develop into typical tentacular zooids.

The surface of a sea scallop shell can act as a base for settling planulae. Once attached, the zooids grow from a stoloniferous network of anastomosing tubes to develop into a colony. The coenosarcal expansion is covered with a heavy, chitinous perisarc from which rise the ridged and jagged spines characteristic of the encrusting colony. Nutritive zooids are the most numerous; other types include defensive, sensory, and generative zooids. The mature colony appears as a reddish velvety covering, but feels rough to the touch because of the numerous spines. Batteries of nematocysts in the zooids protect the colony.

ASSOCIATION OF *HYDRACTINIA ECHINATA* AND *PLACOPECTEN MAGELLANICUS*

The size of a colony of *Hydractinia echinata* on the sea scallop varies with the length of time the colony has been established and with the surface area available. Where there is ample surface for expansion, the zooids in the advancing front of the colony tend to be arranged in concentric rows corresponding to the growth marks on the shell. This arrangement was observed by Frederick M. Bayer (personal communication) of the University of Miami, Fla., to whom material was sent for identification; his finding agrees with remarks by Schijfsma (1939) that the course of stolons is influenced by the surface sculpture of the substrate. The colony, by advancing more rapidly than the scallop grows, may eventually arrive at the periphery of the shell and continue around the shell edge. Long, slender zooids, armed heavily with nematocysts, are especially abundant at the advancing edge. Ultimately, the forward elements of the colony come in contact with the extended mantle of the scallop. The mantle withdraws, presumably because of the nematocysts discharged into it.[1] The mantle retreats steadily as the hydroid colony encroaches inward (fig. 1, a–d). Evidence of this sequence is seen clearly in figure 1, a. To be noted are the numerous relatively

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[1] In section, the nematocysts were found to be about 10 microns long and 4 microns wide and the thread was about at the limit of visibility with an ordinary light microscope. Thus a thread in the scallop mantle cannot be distinguished with the histological technique used. The scallop mantle did, however, show evidence of an inflammatory response (personal communication, Clyde Dawe, National Institutes of Health, Bethesda, Md.). This response was indicated by the greatly increased number of cells under the epithelial margin. Dawe considered these to be wandering amoebocytes coming to the site of the insult.

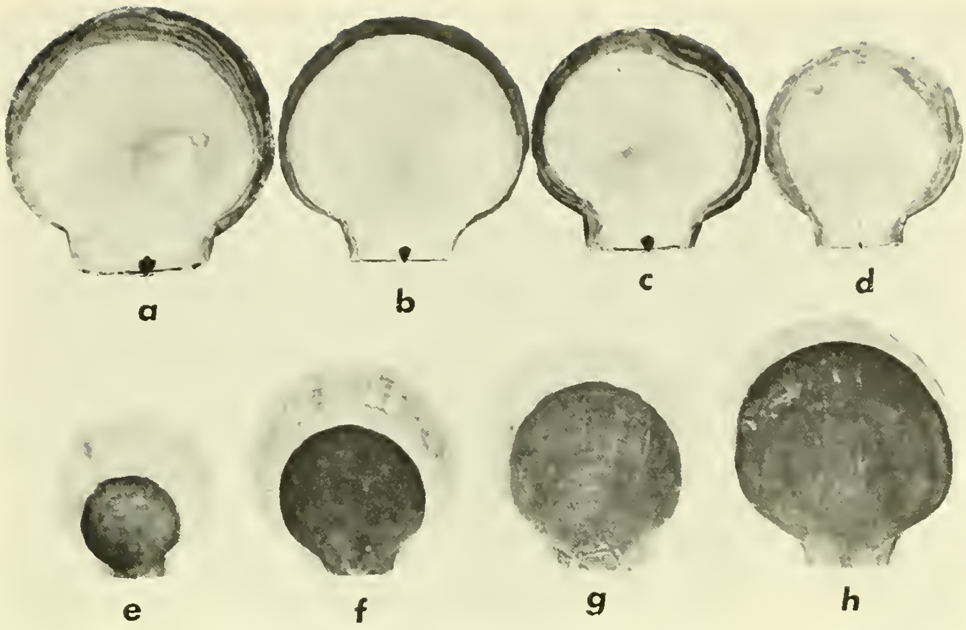

FIGURE 1.—Interior and exterior views of a group of upper (left) valves of *Placopecten magellanicus* showing shell malformation resulting from inner shell invasion by *Hydractinia echinata*. Interior views (a–d) illustrate the persistence of the invading hydroid which causes the scallop to retire further within the shell. External views (e–h) show several scallops that have managed to pass over and grow beyond the hydroids.

thin, slightly irregular, concentric margins secreted by the mantle. Each margin represents successive retreats of the mantle edge.

To resume a normal existence the scallop must successfully overgrow the impinging hydroid colony (fig. 1, e–h). Each time the mantle extends towards the margin it secretes conchiolin, and over this foundation the mantle attempts to produce a new edge of shell over the fringe of the hydroid colony. If it succeeds, shell growth resumes once more. Figure 1b shows an edge of new shell which indicates a successful bridging by the scallop.

A pigment is usually produced in the outer shell layer of the left (upper) valve of the sea scallop. Under some conditions, such as a serious break at the edge of the shell, a scallop secretes new shell material quickly, omitting pigment production until a repair is made and growth becomes normal. The reduction or lack of pigment in scallops as they grow a new lip (fig. 1, e–h) indicates faster rate of shell deposition than usual.

Sometimes a scallop is forced to produce a new edge over the hydroid more than once. Figure 2 shows a scallop that had grown several new shell margins. This is an extreme example but it does illustrate the result of difficulties that sometimes confront scallops. A young scallop increases the periphery of its shell faster than an older one (fig. 1, e) and thus has a better chance to stay ahead of the advancing hydroid.

Hydractinia echinata does not always occupy the entire external shell surface; other epizoons compete for this space as well. Most colonial epizoons live to the severe exclusion of others; it is unusual to see one colony overgrowing another. Usually a distinct zone of demarcation is formed. This also occurs when two colonies of *Hydractinia echinata* meet on the same surface (Schijfsma, 1939). I have examined hundreds of colonies of *Hydractinia echinata* but only once did I find another colonial species growing over the hydroid. This was a granular, encrusting type of unidentified bryozoan spread over the older part of a well-established colony of hydroids. Never was a

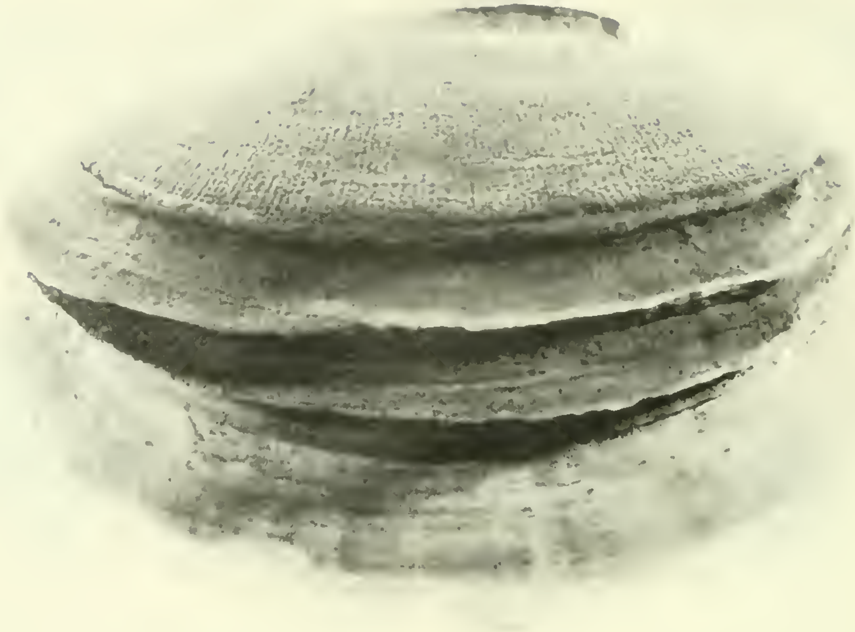

FIGURE 2.—Exterior view of a scallop showing the result when a hydroid colony grows faster than the scallop at successive periods and repeatedly overgrows the shell perimeter.

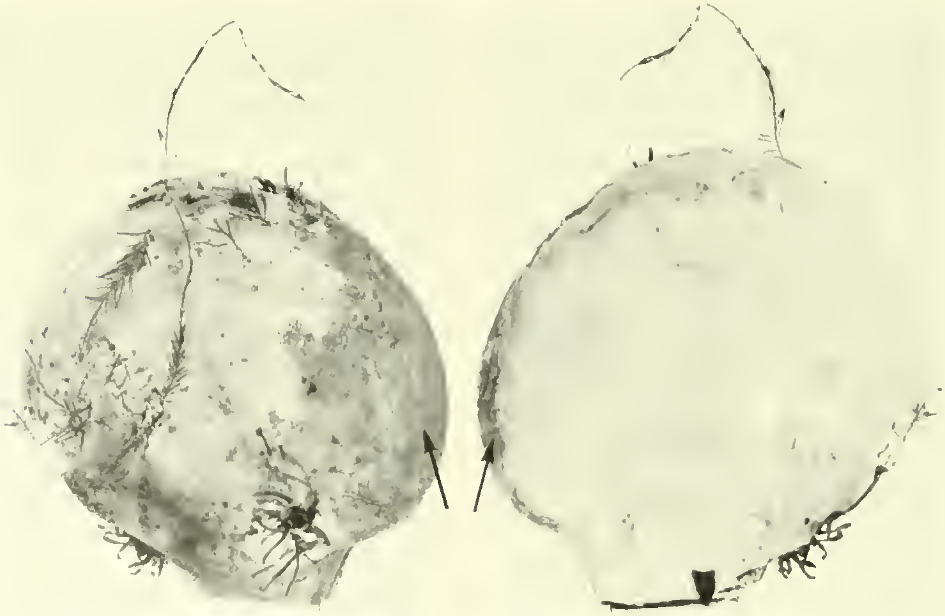

FIGURE 3.—Exterior and interior view of the upper (left) valve of a scallop showing the hydroid partially covering and overgrowing the anterior part of the shell (arrows) causing the scallop to change its shape as it grows in a direction away from the hydroid. (Most fouling organisms were cleaned from the shell before the photo was taken; only chitinous growths remain, including the colonial hydroid, worm tubing, and filamentous hydroids.)

colony of *Hydractinia echinata* seen expanding over another colonial species.

Because of competition with other epizoons, the hydroid often can occupy only a relatively small area of scallop shell surface, hence can inhibit scallop growth over only a relatively small area of the mantle periphery. Limited invasion along the anterior or posterior edge of the shell results frequently in a change in symmetry of the growing scallop; the shell tends to grow more rapidly in a direction away from the disturbed region. Figure 3 shows the interior and exterior view of a scallop shell on which a hydroid that overgrew a short segment of the edge produced a shift in the growth axis. (Note the excavations and deterioration of the shell caused by boring annelids.)

In several instances, expanding colonies of hydroids extended up the plates of barnacles which were also attached to scallop shells. Were they simply seeking additional substrate or did the water currents, created by the feeding barnacles, attract them? Schijfsma (1939) concluded that water currents influence the direction of growth of the colony. Certainly water currents created by a scallop effectively direct growth of a colony toward the shell periphery. Numerous scallops were seen on which the hydroid colony, with equal opportunity to expand in any direction, grew towards the periphery, even obliquely crossing growth lines on the shell in the process.

EFFECTS OF THE ASSOCIATION

Natural mortality of sea scallops, as determined by the ratio of clapper[2] shells to live shells, was uncommonly high in 1960–62 on parts of the important commercial grounds of Georges Bank, off Cape Cod, Mass. (Merrill and Posgay, 1964). We were naturally concerned with the possibility that the hydroid might be responsible for part of this mortality; therefore, during research cruises to Georges Bank in August and September 1961, frequency estimates of *Placopecten magellanicus* and *Hydractinia echinata* were made at all stations where the two species occurred together. Also samples of quick-frozen material from areas of high natural mortality and from areas of high hydroid occurrence were taken to the laboratory for further analyses.

A summary of the results of the analyses is shown in table 1. Samples 1 and 2 are from areas of high hydroid-scallop frequency as reflected by the numbers of hydroids on live and clapper scallops. Samples 3 and 4 are from areas of high clapper–live shell ratios and show a much lower incidence of hydroids. These data make it obvious that the incidence of hydroids and clappers in the same population of sea scallops is not necessarily correlated.

TABLE 1.—*Incidence of occurrence of* Hydractinia echinata *on live and clapper shells of* Placopecten magellanicus

[Samples taken during M/V Delaware cruises 61-13 and 61-16]

Date	Sample number	Location		Number of scallops without hydroids		Number of scallops with hydroids	
		Latitude W.	Longitude N.	Live	Clapper	Live	Clapper
1961				*No.*	*No.*	*No.*	*No.*
Aug. 15	1	41°54.0′	66°39.8′	634	4	208	25
Sept. 24	2	41°53.0′	66°45.9′	300	0	272	16
Aug. 18	3	42°06.1′	66°40.1′	1,123	515	2	1
Sept. 25	4	41°47.1′	66°22.4′	341	42	30	12

Still more apparent is the lack of correlation in the distribution of *Hydractinia echinata* and clappers (fig. 4). As indicated by the darkened area on the chart in Figure 4, areas of high clapper concentration (clapper ratios over 10 percent) in 1961 generally rimmed the

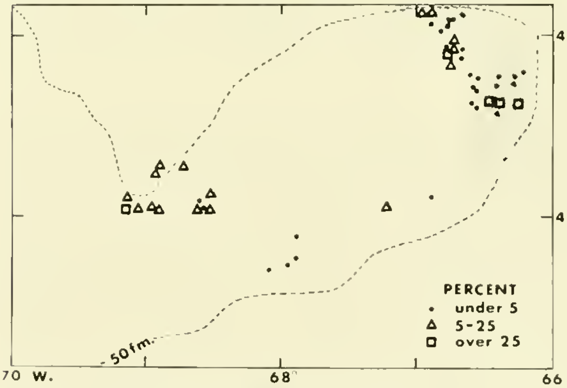

FIGURE 4.—Chart of Georges Bank showing the distribution and density of *Hydractinia echinata* on *Placopecten magellanicus* (symbols) at Georges Bank in relation to the area encompassing high natural mortality in the sea scallop in 1961 (darkened area). Percentage of hydroids on sea scallops indicated.

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[2] The ligament (resilium) holds together the upper and lower valves of a scallop for a period of time after the scallop dies. In this state the shell is referred to as a "clapper."

perimeter from the northern to the lower eastern part of Georges Bank, mostly in depths of 40 to 50 fathoms (73 to 92 m.). Hydroids on scallops in this area, however, were distributed in a more or less straight line from the northern to the eastern part. Furthermore, a high incidence of scallop-hydroid association was found in the western part of Georges Bank where natural mortality was relatively low (fig. 4).

In summary, it can be stated that *Hydractinia echinata* inhibits the sea scallop, but no proof has been found that the hydroid causes the death of scallops.

ASSOCIATION OF *HYDRACTINIA ECHINATA* AND OTHER MOLLUSKS

One colony of hydroids was found partially covering the shell of a 10-mm. pelecypod, *Anomia aculeata* Gmelin, that was attached to the shell of the sea scallop. Careful dissection of the perisarc in this area revealed the shell remains of two other *A. aculeata*, both less than 2 mm. in diameter, completely covered by the colony. *Anomia* attaches to a surface by a partly calcified byssal plug that passes through the bottom shell valve. After the animal dies and the soft parts decompose, the valves soon separate and wash away. As the two valves of both animals were still intact, it appears that the young *Anomia* may have been completely enveloped and smothered by the invader. This circumstantial evidence suggests that mortality of a pelecypod can be attributed to *Hydractinia echinata.*

Gastropod shells also may be occupied by *Hydractinia echinata*. Dead shells of *Nassarius trivittatus* (Say), *Lunatia heros* (Say), *Buccinum undatum* Linnaeus, *Acirsa costulata* (Mighels and Adams), *Colus pygmaea* (Gould), and *Epitonium greenlandicus* (Perry) dredged from the Northern Edge of Georges Bank were covered with *Hydractinia echinata*. The shell apertures were badly deformed, greatly enlarged, and globose. A survey of a large assortment of *Nassarius trivittatus* in the mollusk collection of the Museum of Comparative Zoology at Harvard University revealed several other specimens almost identical to the disfigured ones described above. Apparently this phenomenon is not particularly unusual in nature. Until recently I believed that these deformities of gastropod shell apertures were due to adverse relation between gastropods and hydroids (Merrill, 1964). Further field observations and literature research show, however, that I was wrong. The hydroid grows out on the mouth of the shell only after the snail is dead and only when a pagurid crab inhabits the shell. The deformed and enlarged portion of the shell is made of two layers, the lower by glands of the pagurid, the upper by the hydroid (Aurivillius, 1891). This, then, is a symbiotic association. Enlarging the domain is advantageous to both animals.

One other interesting observation was made regarding the association of *Nassarius trivittatus* and *Hydractinia echinata*. In one dredge haul during R V *DELAWARE* Cruise 62-7 (station 27, south of Nantucket (lat. 41°11′ N.; long. 70°16′ W.) on June 16, 1962, in 15 fathoms (27 m.)) many live specimens of *Buccinum undatum* were taken. Most of the specimens had colonies of *Hydractinia echinata*. On top of some of the colonies, *N. trivittatus* had deposited masses of egg cases. Evidently the organs necessary for locomotion and egg laying in gastropods are not as sensitive as the mantle in pelecypods to the defensive elements of the hydroid.

CONCLUSIONS AND SUMMARY

Hydractinia echinata frequently lives as an epizoon on the shell of the sea scallop, *Placopecten magellanicus*. It often expands over and around the margin of the shell and interferes with the normal mantle activity of the host. This interference in turn affects normal metabolism and can cause shell malformation. Mortality possibly attributable to this hydroid was noted in a pelecypod, *Anomia aculeata*, as was deformity of many gastropod shells. Thus, *Hydractinia echinata*, which normally uses a shell only as a substrate, is capable of becoming a harmful epizoon.

Geographic distribution of scallops in areas of known high natural mortality and areas of high hydroid occurrence were analyzed to determine the possibility that the hydroid is an epizootic agent. A lack of correlation indicated that the hydroid was not the cause of the heavy natural mortality of scallops.

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OFFSHORE DISTRIBUTION OF *HYDRACTINIA ECHINATA*

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ABSTRACT

New distributional records for this hydroid are listed from 81 offshore locations along the Middle Atlantic region and from Georges Bank, off Massachusetts. The species was commonly found living on the shells of animals having some degree of mobility—sea scallops (*Placopecten magellanicus*), and gastropod shells inhabited by pagurid crabs. The bottom substrate for these animals is predominantly gravelly—a mixture of sand, pebble, and shell. Depths at sampling stations ranged from 16 to 80 fathoms; depths where the hydroid occurred ranged from 16 to 62 fathoms. Deeper stations had soft substrates containing silt and clay, unsuitable for semimotile animals and lacking the hard substrate necessary for hydroid colonization.

Hydractinia echinata (Fleming) is circumpolar in its principal distribution (Fraser, 1946). Fraser (1944) documented the distribution of this hydroid in the western Atlantic, mostly in shoal waters from Salmon Bay, Labrador, to Charleston Harbor, S.C. He recorded numerous locations around the New England coast but none from Georges Bank, although he did include a locality from Georges Basin, near Georges Bank. Only a few scattered and inshore localities were listed for the great Middle Atlantic region. Deevey (1950) extended the range to the Gulf of Mexico.

The purpose of this paper is to describe the bathymetric distribution of *Hydractinia echinata*. Eighty-one new locations on Georges Bank, off Massachusetts, and on the continental shelf of the middle Atlantic bight from depths of 16 to 62 fathoms (fig. 1), complement Fraser's (1944) records from Cape Cod northward. I acquired these data while on research cruises relating to the sea scallop, *Placopecten magellanicus* (Gmelin) (Merrill, 1962; Merrill and Posgay, 1964). This paper is part of a general study to evaluate the significance of an adverse effect of this hydroid epizoon on the commercially important sea scallop (Merrill, 1967).

The hydroid was found colonizing the shells of live sea scallops and the shells of gastropods occupied by pagurid crabs. The scallops and crabs are mobile and inhabit hard rather than soft bottom. Generally, the substrates of stations shallower than 60 fathoms were predominantly sand, pebble, and shell, whereas those deeper than 60 fathoms contained much silt and clay. Depths of the sampling stations ranged from 16 to 80 fathoms. The deepest record for the hydroid was 62 fathoms, which coincided with the greatest depth at which scallops and crabs were taken.

Data on the bathymetric range of *Hydractinia echinata* are sparse. Verrill (1885) stated it was common from low water to 60 fathoms. Smith and Harger's (1874) greatest depth was 65 fathoms. Fraser (1944, 1946) reported the following deepwater locations: 42°02′15″ N., 70°15′ N. [sic], Cape Cod Bay, 362 fathoms; 42°03′ N., 70°37′ W., 30 miles off Cape Cod light, 106 fathoms; 52°01′ N., 68°00′30″ W., off Cape Cod, 86 fathoms. The first two positions are shoal waters, under 25 fathoms. Furthermore, Cape Cod has no water 362 fathoms deep, nor has the whole Gulf of Maine. His third location in 86 fathoms is possible.

A few records from Georges Bank have been noted in the literature. Smith and Harger (1874) listed *Hydractinia polyclina* (= *Hydractinia echinata*) from five stations on the Bank near Cultivator Shoal, the Northern

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Edge, and Corsair Canyon.

The stations on Georges Bank (fig. 1) were made during M/V *Delaware* cruise 61–16, September 22-30, 1961, where *Hydractinia echinata* was found on the shell of *Placopecten magellanicus* (Merrill and Posgay, 1964) in depths from 77 to 136 m. The stations covered most of Georges Bank except the northwest part where few scallops are taken.

Several other locations on Georges Bank where hydroids and sea scallops have been found associated are on figure 1. The records are mostly the result of miscellaneous samples brought to the laboratory.

I looked for *Hydractinia echinata* on gastropod shells inhabited by hermit crabs during a cruise (M/V *Delaware* cruise 60–7) along the middle Atlantic from Block Island to Cape Hatteras, mostly in depths of 20 to 80 fathoms, May 11-21, 1960. The purpose of the cruise was to determine the distribution of sea scallops and other invertebrates. Pertinent information regarding the cruise was given by Merrill (1962). Stations where gastropod shells and hydroids occurred together are plotted in figure 1. The hydroids were found in depths from 16 to 40 fathoms on shells of *Nassarius trivittatus* (Say), *Lunatia triseriata* (Say), *Lunatia heros* (Say), *Colus pygmaeus* (Gould), *Colus stimpsoni* (Mörch), and *Bucci-*

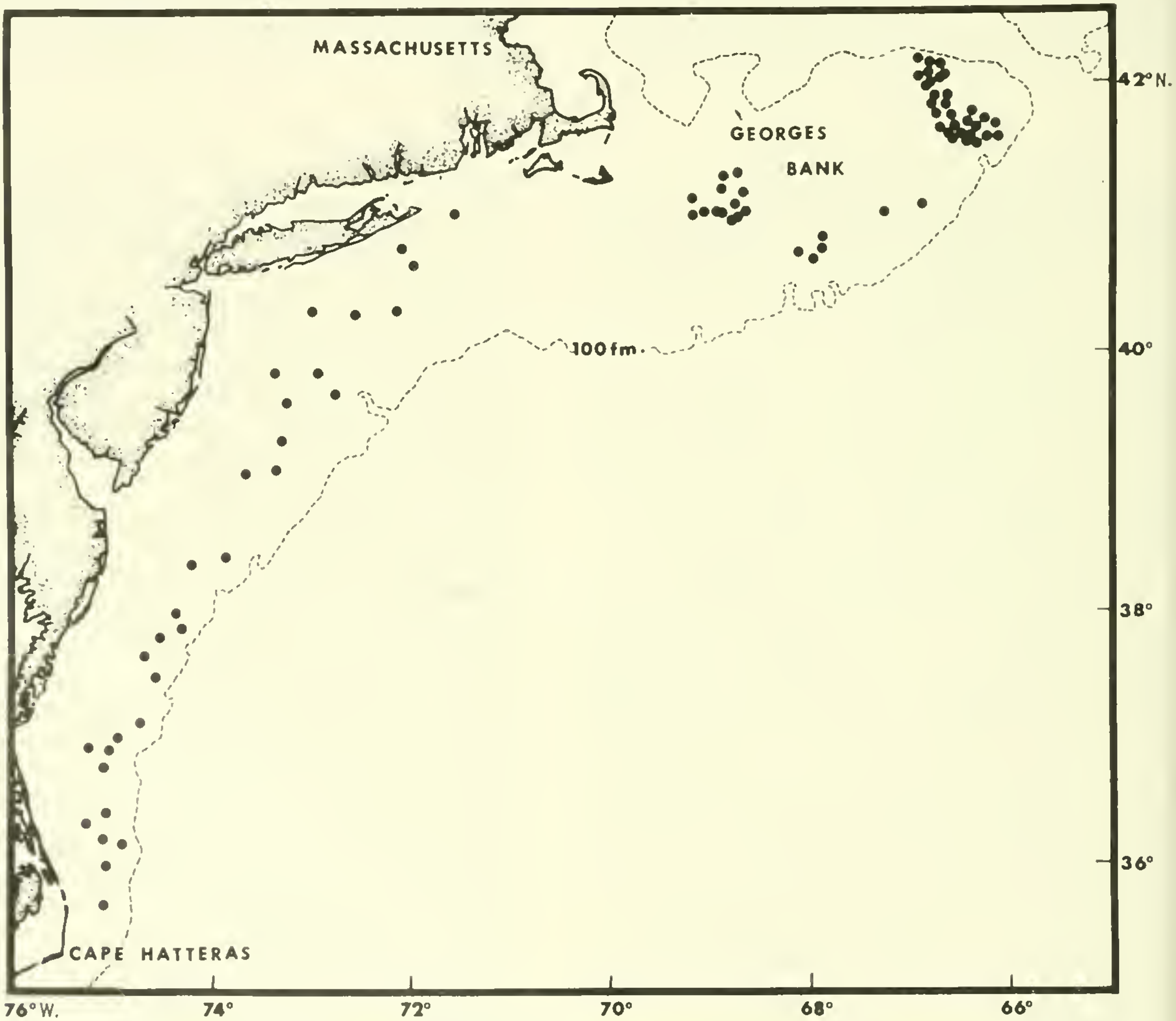

FIGURE 1.—Distribution of the hydroid, *Hydractinia echinata*, in the Georges Bank and middle Atlantic areas. Circles represent locations where the hyroid was taken.

num undatum Linné which were occupied either by *Pagurus bernhardus acadianus* (Benedict) or by *Pagurus pollicaris* (Say).[1]

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[1] Pagurids identified by Anthony J. Provenzano, Jr., University of Miami, Miami, Fla.

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CYCLOPOID COPEPODS OF THE GENUS *TUCCA* (TUCCIDAE), PARASITIC ON DIODONTID AND TETRAODONTID FISHES

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ABSTRACT

The female of *Tucca impressus* Krøyer is redescribed, on the basis of specimens taken from *Chilomycterus schoepfi* (Walbaum) in the Gulf of Mexico. Both genus *Tucca* Krøyer and family Tuccidae Vervoort are redefined, and the genus is treated as monotypic. A restudy of the specimens in the U.S. National Museum revealed that *T. corpulentus* Wilson should be synonymized with *T. impressus* and that the males of *T. impressus* described by Wilson (1911) are actually some immature adult females of the same species before complete metamorphosis.

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome; the second pedigerous segment and the urosome remain unchanged. The metamorphosis is widening rather than lengthening in the head, but more lengthening than widening in the trunk.

Some geographical variation in size and shape is observed in the metamorphosed parts of the body. The three recognized geographical types are: Atlantic type (with slightly bilobed lateral wings of head and less prominent posterior lobes in trunk), Gulf type (with unlobed lateral wings of head and less prominent posterior lobes in trunk), and Caribbean type (with prominent bilobed lateral wings of head and posterior lobes in trunk). This variation is not strictly expressed, however, by every individual in a given geographical range.

This study was developed from the identification of two specimens of immature adult females of *Tucca impressus* Krøyer, which were collected from the caudal fin of a spiny boxfish, *Chilomycterus schoepfi* (Walbaum), at Alligator Harbor, Fla. The specimens were collected by Jack Rudloe and sent to William A. Newman, Museum of Comparative Zoology, Harvard University, for identification, and subsequently were passed to me through Arthur G. Humes, Department of Biology, Boston University, in May 1965. Because my observations on these two parasites were so different from the description by Wilson (1911), five more collections were obtained and studied. In addition, I reexamined the specimens in the USNM (U. S. National Museum) which were studied by Wilson. This reexamination revealed that Wilson (1911) had introduced errors into our knowledge of the species of the genus *Tucca* Krøyer. The later establishment of a subfamily (by Vervoort, 1962) and family (by Yamaguti, 1963) to contain *Tucca* is based on the information supplied by Wilson.

A redescription of the species and redefinition of the genus and the family are given here. Observations on metamorphosis and geographical variation in morphology are also included.

The redescription of the female of *T. impressus* given below is mainly based on specimens collected off Cape San Blas, in the Gulf of Mexico, because this collection is the largest of my collections, contains numerous females in various stages of growth, and indicates a certain pattern of metamorphosis. The data given in tables 2, 3, and 4 were prepared from this collection to aid in the explanation of metamorphosis.

After the discovery of a certain degree of geographical variation of *T. impressus,* tables 5 and 6 were prepared from the two largest collections in the USNM, one from North Carolina and the other from Jamaica. Table 4 gives data on the specimens taken from the Gulf of Mexico, which also helps to explain geographical variation.

The specimens were dissected and examined in lactic acid, and the figures were drawn with the aid of a camera lucida.

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SYSTEMATIC ACCOUNT

FAMILY TUCCIDAE VERVOORT, 1962

Diagnosis

Female. — Metamorphosed cyclopoid. Body composed of head, neck, trunk, and "tail." Head formed by fusion of cephalosome and first pedigerous segment, globular dorsally, flattened and hollowed ventrally, and winged laterally. Cephalic appendages and first leg housed in ventral concavity. Neck short, wider than long, formed by second pedigerous segment, distinctly separated from trunk posteriorly. Trunk composed of fused third and fourth pedigerous segments, inflated, much wider than head and neck. "Tail" composed of transformed urosome with all segments completely fused, flattened, wider than long, attached posteroventrally to trunk. Caudal rami small. Eggs multiserate; egg sacs elongate, cylindrical.

First antenna 5- or 6-segmented, with numerous setae. Second antenna 3-segmented; terminal segment armed, in addition to claws and setae, with pectinate, lamelliform process at tip and several rows of teeth or scales over posterior surface. Labrum with marginal teeth; labium weakly developed. Mandible elongate, with two denticulated spines. Paragnath present. First maxilla a small, rounded protrusion, bearing four setae. Second maxilla 2-segmented, tipped with three denticulated spines. Maxilliped indistinctly 3-segmented, terminal segment strongly bent and pointed. Four pairs of biramous legs; rami with reduced segments. Leg five, 1-segmented, segment very small, tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

This family contains but a single genus, *Tucca* Krøyer, 1837. The genus *Tuccopsis* Pearse, 1952, which was included in the family by Yamaguti (1963), is synonymous with *Blias* Krøyer, 1864, of the family Chondracanthidae. This synonymy was first pointed out by Causey (1955: 7) and followed by Vervoort (1962: 93).

When Vervoort (1962) reviewed the family Bomolochidae, he included the genus *Tucca*, following Wilson's (1911) opinion, but he set the genus in a new subfamily Tuccinae. Since Vervoort did not himself examine specimens of the genus *Tucca*, his accounts on the Tuccinae Vervoort, *Tucca* Krøyer, *T. impressus* Krøyer, *T. corpulentus* Wilson, and *T. verrucosus* Wilson were wholly based on Wilson's inaccurate observations (see Remarks in the following two sections). Yamaguti's (1963) account was also based entirely on Wilson's descriptions. Therefore, neither the diagnosis of the family Tuccidae given by Yamaguti (1963: 42) nor the diagnosis of the subfamily Tuccinae given by Vervoort (1962: 92) can be adopted here. The status of the family is then: a redefined family Tuccidae Yamaguti, 1963, embracing within it the redefined and promoted subfamily Tuccinae Vervoort, 1962.

Wilson (1911: 353) pointed out that the copepods of the genus *Tucca* are closely related to the bomolochid copepods, a relationship especially suggested by the mouth parts and other cephalic appendages. I consider the following characteristics of the female of the genus *Tucca*, however, so different from those of the bomolochids that *Tucca* should be placed in a different family:

1. The female undergoes metamorphosis after the last copepodid stage. All known bomolochids (this means all the copepods attributed to the subfamily Bomolochinae by Vervoort in 1962) have no metamorphosis, and all have a cyclopoid form of body. In the tuccids, however, a metamorphosed adult female has its body distinctly separated into head, neck, and "tail;" the appearance is not at all cyclopoid.

2. The urosome of the female is rudimentary, its length less than one tenth of the body. The urosome of the bomolochids is always at least one third as long as the body and distinctly 5-segmented; it comprises a fifth pedigerous segment, a genital segment, and three postgenital segments. Tuccids have a rudimentary fifth pedigerous segment, a genital segment, and a single postgenital segment, all fused into one unit and unsegmented.

3. The fifth leg is very rudimentary, merely a small, single segment armed with three setae. The fifth leg of a typical bomolochid is 2-segmented and consists of a small intermediate

segment and a large spatulate, terminal segment; even in those with a 1-segmented fifth leg, such as the species of *Pseudocucanthus* Brian and *Orbitacolax* Shen, the free segment is still well developed and spatulate. The terminal, spatulate segment of the bomolochids is usually armed with one spine on the outer surface and two spines and one seta at the distal end.

GENUS *TUCCA* KRØYER, 1837

Diagnosis

Type species is *Tucca impressus* Krøyer, 1837.

Female.—Body form and mouth parts as defined for the family. Eggs multiserate; egg sacs cylindrical, longer than body. First antenna 5- or indistinctly 6-segmented, basal segment armed with a strong hook on ventral surface. Second antenna 3-segmented, bearing terminally five weak claws, three setae, and one pectinate, lamelliform process; distal segment covered with teeth posteriorly. Leg 1 biramous, flattened, and 3-segmented, located on posterior wall of ventral concavity in head. Leg 2 biramous, 2-segmented. Leg 3 and leg 4 with 2-segmented exopod and 1-segmented endopod; intercoxal plate missing. Leg 5 very small, a single segment tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

When Krøyer (1837) established this genus, he gave almost no account of the appendages, and neither did Nordmann (1864) in his description of West African specimens that he called *T. impressus*. Consequently, lacking such information, these authors were inconsistent in the familial attribution of the genus *Tucca*. Krøyer placed it in the family Dichelestiidae and Nordmann in the famliy Chondracanthidae. Both Milne-Edwards (1840) and Bassett-Smith (1899) followed Krøyer's opinion.

The nature of the mouth parts of *Tucca* was not known until 1911, when Wilson studied the specimens of *Tucca* in the collections of the U.S. National Museum. According to his observations, he placed the genus in the subfamily Bomolochinae of the family Ergasilidae, but later, in 1932, he promoted the subfamily to the familial level.

Wilson's additional information on the morphology of the species of *Tucca* was, however, correct only in the gross anatomy of the mouth parts and not entirely right in the fine structures of the mouth parts and other appendages. I discovered these errors after restudying the specimens of *Tucca* that had been studied by Wilson in 1911 (the collections from Woods Hole, Mass., and Beaufort, N.C.), in 1913 (the collections from Montego Bay, Jamaica), and in 1932 (the collections from Woods Hole, Mass.). The new species, *Tucca corpulentus*, described by him, is only a deformed specimen of *T. impressus;* and some immature adult females of *T. impressus* were mistaken by him for adult males. As Vervoort (1962: 93–96) and Yamaguti (1963: 43–44) were misled by Wilson's inaccurate observations, their accounts of the species of the genus *Tucca* should be used with reservations. This problem is discussed in more detail in a later section.

The specimens described by Nordmann (1864: 491–494, pl. VI, figs. 7–10) as *T. impressus* were claimed by Wilson (1911: 359–360) to be a new species, to which he gave the name *T. verrucosus*. I refrain from making any decision on the validity of *T. verrucosus* without consulting either the original material studied by Nordmann or other specimens collected from the same locality (west coast of Africa) and the same host (*Diodon* sp.). If Wilson's assumption is correct, then *T. verrucosus* would naturally be the second species of the genus; however, I now prefer to treat the genus as monotypic.

A doubtful form, *Tucca* sp., was introduced to the genus by Pearse (1952: 12, figs. 23–27). This species, however, has been questioned by Causey (1955: 11) as being probably a mutilated specimen of *Blias prionoti* Krøyer, 1864. The mandible of Pearse's *Tucca* sp. is very convincing evidence that it is not a tuccid. Its form of a "slightly curved hook" indicates a chondracanthid type of mandible rather than a tuccid type.

TUCCA IMPRESSUS KRØYER, 1837

Tucca impressus Krøyer, 1837, pp. 479–482, pl. V, fig. 2 (a–h). Milne-Edwards, 1840, p. 496. Bassett-Smith, 1899, p, 469. Wilson, 1908, p.

625; 1911. pp. 354–387, pl. 48, figs. 102–108, pl. 49, figs. 109–115, 118–120; 1913, p. 200; 1932, pp. 379–380, fig. 243(a,b). Bere, 1936, p. 582. Heegaard, 1947, pl. 25, fig. 195. Sewell, 1949, p. 157. Carvalho, 1951, p. 136. Pearse, 1952, p. 191. Causey, 1955, p. 3. Vervoort, 1962, pp. 93–95. Yamaguti, 1963, p. 43, pl. 47, figs. 1(a–k).

Tucca corpulentus Wilson, 1911, pp. 358–359, pl. 49, figs. 116, 117, pl. 50, figs. 121–127; 1932, pp. 380–381, fig. 235 (a,b). Heegaard, 1947, pl. 25, fig. 194. Sewell, 1949, p. 157. Veervoort, 1962, pp. 95–96. Yamaguti, 1963, p. 43, pl. 46, fig. 1(a–g).

Material Examined

Two immature adult females from caudal fins of 2 *Chilomycterus schoepfi*, caught in mullet seine, at Alligator Harbor, Fla., March 1965; 7 ovigerous females, 3 immature adult females, and 1 copepodid from fins of three *C. schoepfi*, caught in gill net, at Panacea, Fla., May 14, 1965; 44 ovigerous females, 9 immature adult females, and 2 copepodids taken from 14 *C. schoepfi*, caught in shrimp trawl, off Cape San Blas, Fla., May 16, 1965; 6 ovigerous females on dorsal and pectoral fins of 2 *C. schoepfi*, caught in shrimp trawl, off Carrabelle, Fla., July 18, 1965; 9 ovigerous females from fins and body surface of *C. schoepfi*, caught in shrimp trawl by R/V *Oregon*, off St. Simons Island, Ga., November 17, 1965.

In addition to the above collections, I examined the following 16 collections in the USNM (the host names for USNM 38619, 38628, 47748, and 74375 are here changed from *C. geometricus* to *C. schoepfi*):

6090—3 adult females "from exterior surface of rough swellfish, P. Stewart's pound," Woods Hole, Mass., July 26, 1882.

38369—3 adult females and 3 immature adult females from fins of *C. schoepfi*, collected in Louisiana by M. H. Spaulding, August 10, 1907.

38625—8 adult females and 3 immature adult females from fins of *C. schoepfi*, collected at Beaufort, N.C., in 1904.

38627—8 adult females from pectoral fins of *C. schoepfi*, collected at Beaufort, N.C., in 1905.

38628—11 adult females from pectoral fins of *C. schoepfi*, collected at Beaufort, N.C., in 1902.

42251—7 adult females from fins of *C. antennatus* (Cuvier), collected at Montego Bay, Jamaica, June 22, 1910.

42264—5 adult females from pectoral fins of *Diodon hystrix* Linnaeus, collected at Montego Bay, Jamaica, June 22, 1910.

42265—2 immature adult females from pectoral fins of *Spheroides marmoratus* (Ranzani), collected at Montego Bay, Jamaica, June 20, 1910.

42269—1 deformed immature female on fin of *S. marmoratus*, collected at Montego Bay, Jamaica, September 15, 1910.

42273—57 adult females, 1 immature adult female, and 1 copepodid from fins of *C. antennatus*, collected at Montego Bay, Jamaica, June 15, 1910.

47748—19 adult females from *C. schoepfi*, collected at Morehead City, N.C., April 7, 1891.

53525—5 adult females from Beaufort, N.C. (no host or date given).

74375—7 adult females on fins of *C. schoepfi*, collected at Beaufort, N.C., August 1905.

79089—2 adult females under pectoral fin of *C. spinosus* (Linnaeus), collected at Lemon Bay, Fla., in 1934–35.

The following two collections from USNM are labeled as *Tucca corpulentus:*

38619—"Type," 2 adult females (1 decapitated) from fins of *C. schoepfi*, collected at Woods Hole, Mass., in 1887 (see Remarks).

79595—3 adult females on gill of *S. maculatus* (Bloch and Schneider), collected at Woods Hole, Mass., by G. A. Maccallum (no date given; see Remarks).

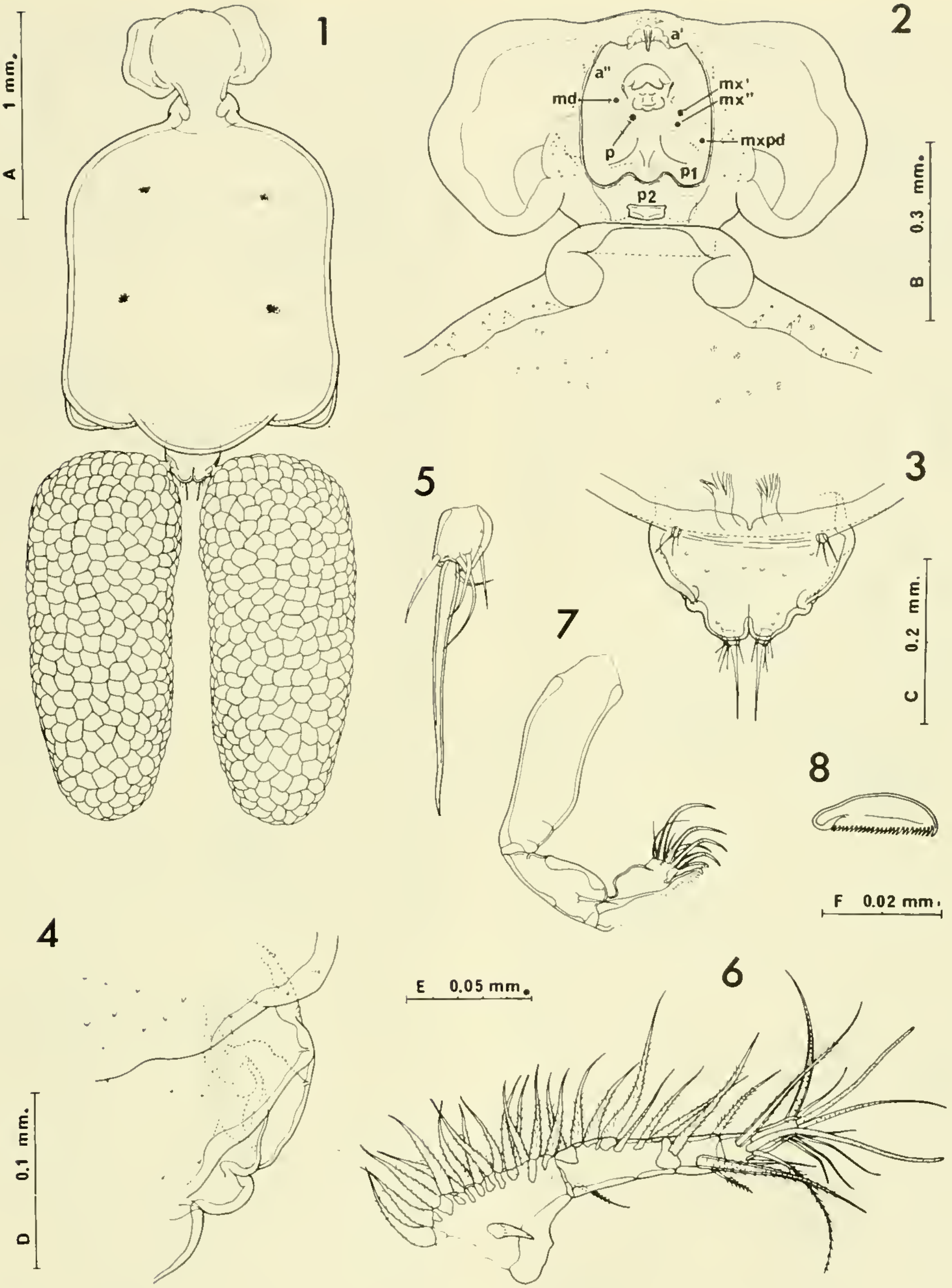
Distribution

See table 1.

TABLE 1.—*Hosts and distribution of* Tucca impressus [1]

Host	Locality	Collection of	Authority
Family Tetraodontidae			
Spheroides maculotus.	Woods Hole, Mass	USNM 6090	Wilson (?)
S. mormoratus	Montego Bay, Jamaica	USNM 42265	Do. (1913)
		USNM 42269	Do. (1913)
Family Diodontidae			
Diodon hystrix	Danish West Indies	?	Krøyer (1837)
	Montego Bay, Jamaica	USNM 42264	Wilson (1913)
Chilomycterus antennatus.	Montego Bay, Jamaica	USNM 42251	Do. (1913)
		USNM 42273	Do. (1913)
C. schoepfi	Woods Hole, Mass	USNM 38619	Do. (1911)
	Beaufort, N.C	USNM 38625	Do. (1911)
		USNM 38627	Do. (1911)
		USNM 38628	Do. (1911)
	Louisiana	USNM 38369	Do. (?)
	Morehead City, N.C	USNM 47748	Do. (?)
	Beaufort, N.C	USNM 74375	Do. (?)
	Sao Paulo, Brazil	?	Carvalho (1951)
	Alligator Harbor, Fla	?	Pearse (1952)
	Pascagoula, Miss	Author	Causey (1955)
	Panacea, Fla	do	Present paper
	Cape San Blas, Fla	do	Do. paper
	Carrabelle, Fla	do	Do. paper
	St. Simons Island, Ga	do	Do. paper
C. spinosus	Lemon Bay, Fla	USNM 79089	Bere (1936)

[1] Nordmann's record of *Tucca impressus* from the west coast of Africa is excluded, because of its uncertain identification. USNM 53525 is also not included because the host was not identified.



FIGURES 1–8. *Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla., in the Gulf of Mexico. The letter in the parentheses after the explanation of each figure refers to the scale at which the figure was drawn. 1. Entire, dorsal (A). 2. Head, neck, and anterior end of trunk, showing relative position of various cephalic appendages, ventral (B). 3. "Tail" (= urosome), ventral (C). 4. Genital segment, showing egg sac attachment area, dorsal (D). 5. Caudal ramus, ventral (E). 6. First antenna, exterior (E). 7. Second antenna, exterior (E). 8. Lamelliform process at tip of second antenna, interior (F). (a'.=first antenna; a".=second antenna; md.=mandible; mx'.=first maxilla; mx".=second maxilla; mxpd.=maxilliped; p.=paragnath; p_1.=leg 1; p_2.=leg 2).

Description of Stages

Three stages are described below: mature ovigerous female, immature adult female, and female copepodid.

Mature ovigerous female: — Body (fig. 1) noncyclopoid, 1.51 to 2.92 mm. long, composed of head, neck, trunk, and "tail." Head (fig. 2) small, 0.46 by 0.71 mm., representing a fusion of cephalosome and first pedigerous segment; inflated dorsally, flattened ventrally (fig. 25), and with two wide lobed wings laterally, which in a fully grown adult female protrude beyond anterior margin of cephalosome. Ventral surface of head deeply invaginated at center, forming a hollow disk (fig. 2) which is reinforced anteriorly by rostrum and bases on first antennae and posteriorly by flattened leg 1. Second antennae, mouth parts, and maxillipeds found on bottom of this disk. Rostrum (fig. 2) well developed, bearing some refractile points, two sclerotic protrusions, and one fairly strong hook pointing posteroventrally.

Head jointed to trunk by a short neck (fig. 2) which is formed by second pedigerous segment; this segment completely fused with head anteriorly. This portion of body highly variable in length in different individuals, fully extended in some specimens and completely contracted in others, leaving practically no space between head and trunk. Trunk (fig. 1) made up of third and fourth pedigerous segments, 1.54 by 1.31 mm., nearly square, with rounded corners. Posterior corners slightly produced on each side into one dorsal and one ventral lobe (fig. 25), and a third lobe produced from posteromedial end of trunk between two dorsal lobes. Four depressions (fig. 1) on dorsal surface of trunk. "Tail" (fig. 3) flattened, 0.17 by 0.26 mm., attached to trunk posteroventrally (fig. 25), totally or partially concealed by dorsal posteromedial lobe. No appreciable segmentation seen in "tail," which apparently represents a fusion of the narrow fifth pedigerous segment, the circular genital segment, and one small postgenital segment. Egg sac attachment area (fig. 4) well developed, occupying about two-thirds of lateral surface of "tail." Caudal ramus (fig. 5) small, 23 by 20 μ, armed with five short setules and one long seta 114 μ long. Egg sac elongate, cylindrical; fully grown sac longer than body, containing numerous small eggs with a diameter of 90 μ. Many micropits on surfaces of head and trunk, as shown in detail in figs. 2 and 4, penetrating deeply into sclerotic covering of body.

First antenna (fig. 6) distinctly 5-segmented, but second segment suggesting a division into two segments. Armature on these five segments, from proximal to distal: 15 + 1 hook (on ventral surface), 8, 3, 3, + 1 aesthete, and 7 + 1 aesthete.

Second antenna (fig. 7) 3-segmented; basal segment longest, naked; second segment bearing one seta. Terminal segment having subterminally a rod-shaped process and one pectinate, lamelliform process (fig. 8), and carrying terminally three setae and five weak claws; several rows of teeth on posterior surface.

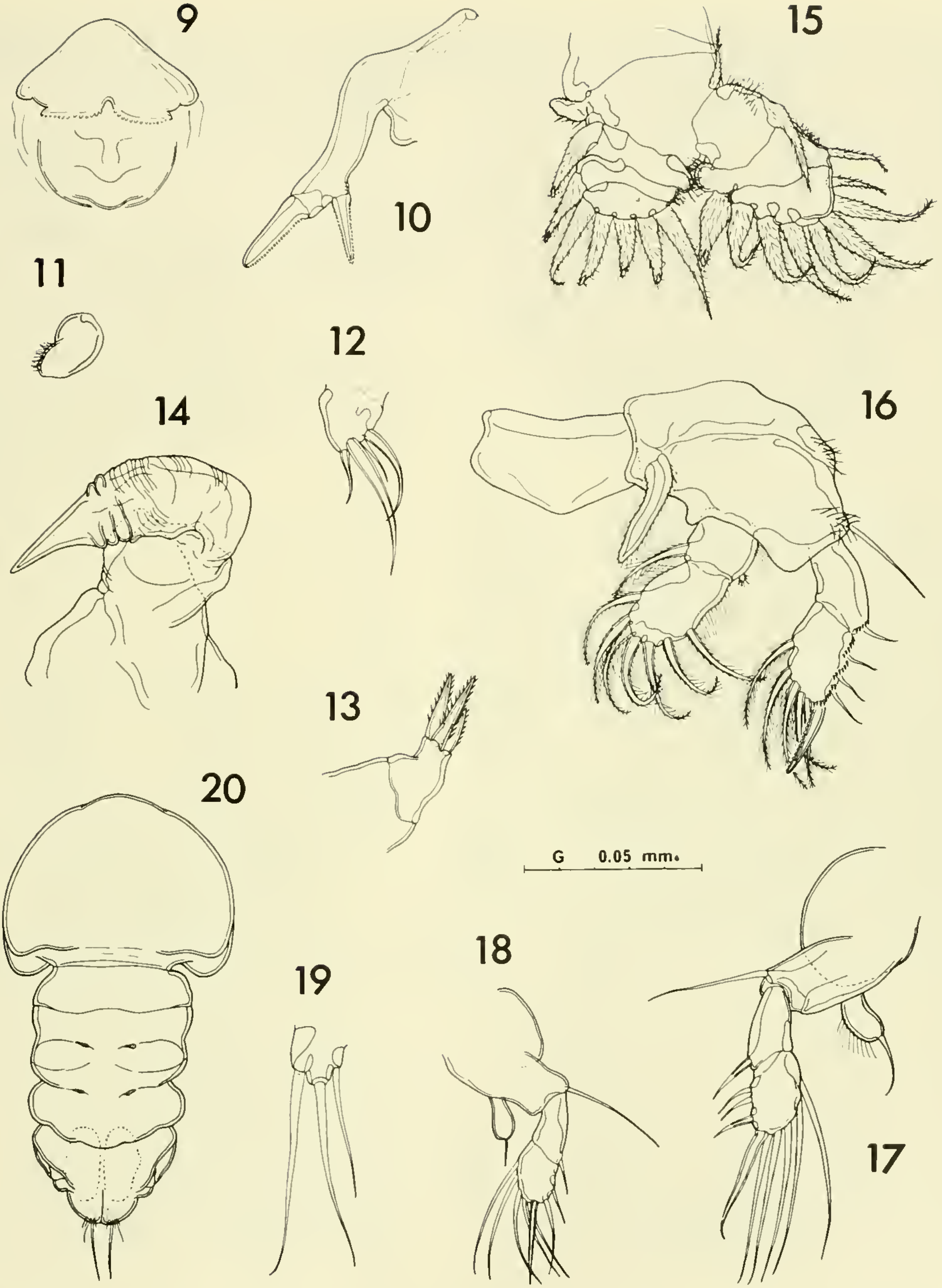
Labrum (fig. 9) well developed, with fine teeth on posterior free margin; labium weak. Mandible (fig. 10) composed of a large plate produced into long process, armed with one terminal masticatory process and one subterminal, bilaterally denticulated spine. Paragnath (fig. 11) bearing setules, located posteromedially to mandible. First maxilla (fig. 12) a small rounded protrusion, located laterally to paragnath, bearing four setae, one of which is fairly long. Second maxilla (fig. 13) 2-segmented, terminal segment armed with three bilaterally denticulated spines.

Maxilliped (fig. 14) powerfully developed, indistinctly 3-segmented; terminal segment strongly bent inward and almost perpendicular to first two segments. Last segment sharply pointed, with well-developed sclerites cutting into ventral and posterior surfaces, thus making these surfaces corrugated. In many specimens, the terminal, pointed process, broken when the parasite was removed from the host, appeared as a blunt process.

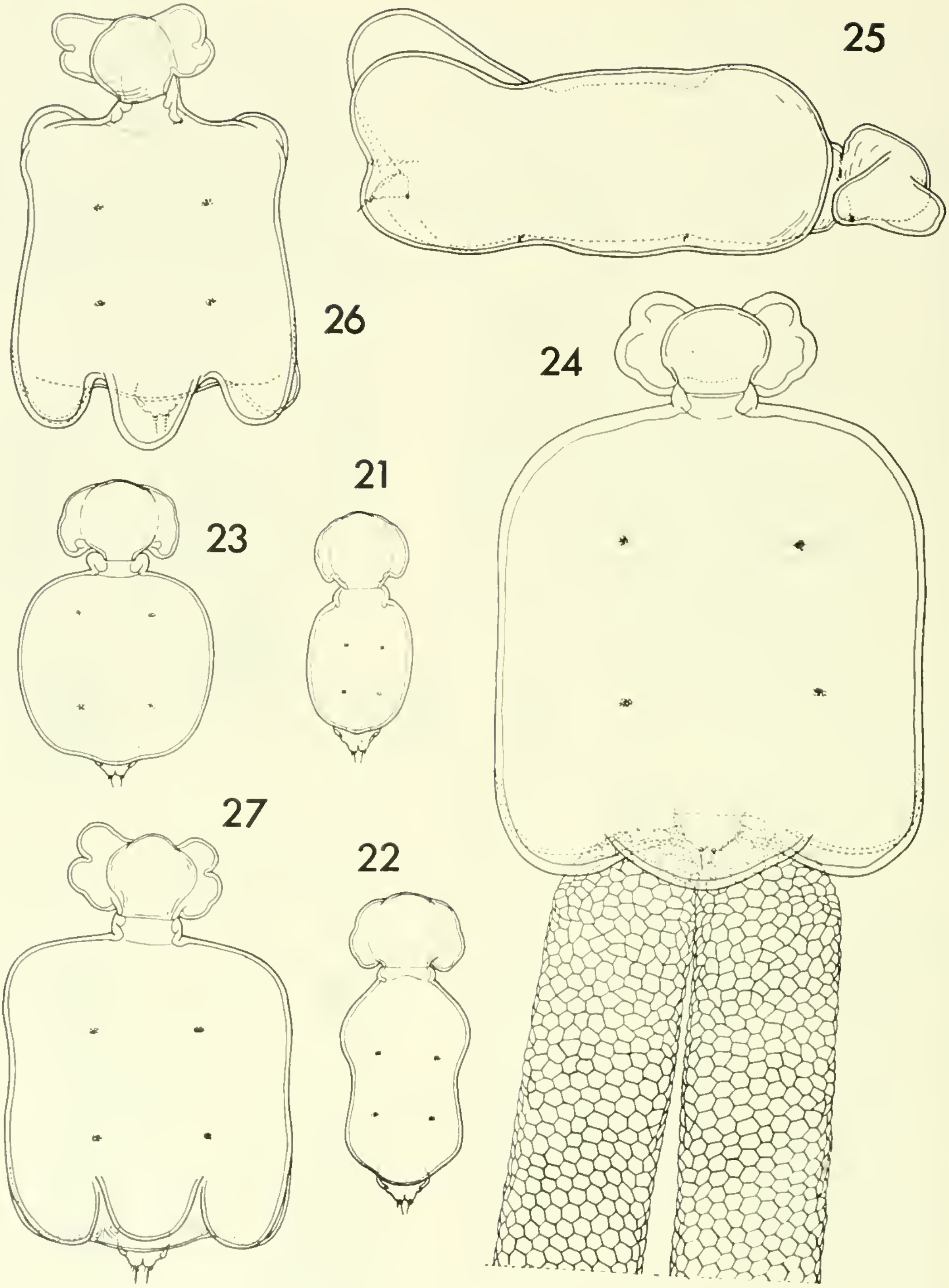
Formula of spines and setae on first four pairs of legs as follows (Arabic numerals represent setae and Roman numerals spines):

	Protopod	Exopod	Endopod
Leg 1	0-0 1-0	1-0 1-1 7	0-1 0-1 5
Leg 2	0-0 1-I	1-0 III-I-5	0-1 7
Leg 3	0-0 1-0	I-0 III-I-5	1
Leg 4	0-0 1-0	I-0 II-I-5	1

Leg 1 (fig. 15) strongly flattened, its setae



Figures 9–20.—*Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla. in the Gulf of Mexico. 9. Labrum and labium, ventral (G). 10. Mandible, posterior (G). 11. Paragnath, ventral (G). 12. First maxilla, anterior (G). 13. Second maxilla, anterior (G). 14. Maxilliped, posteroventral (D). 15. Leg 1, anterior (D). 16. Leg 2 and intercoxal plate, anterior (E). 17. Leg 3, anterior (G). 18. Leg 4, anterior (G). 19. Leg 5, ventral (F). 20. Copepodid, dorsal (B).



FIGURES 21-27.—*Tucca impressus*, female. Figures 21-23, from *Chilomycterus schoepfi* taken off Cape San Blas, in the Gulf of Mexico; 24-25, from *C. schoepfi* taken off St. Simons Island, Ga.; 26-27, from *C. antennatus* at Montego Bay, Jamaica. 21. Immature adult with short trunk, dorsal (A). 22. Immature adult with guitar-shaped trunk, dorsal (A). 23. Immature adult with circular trunk, dorsal (A). 24. Entire, dorsal (A). 25. Same, lateral (egg sacs omitted) (A). 26. Entire, dorsal (egg sacs omitted) (A). 27. Entire, showing absence of anterior lobes in trunk (egg sacs omitted) (A).

densely haired. Medial surface of basis produced into blunt process, covered with hairs; marginal surfaces of every segment in each ramus also covered with hairs. Spines on outer surfaces of exopods of leg 2 (fig. 16), leg 3 (fig. 17), and leg 4 (fig. 18) weakly developed, setiform, and naked. Intercoxal plate absent in leg 1, leg 3, and leg 4; coxa and basis not completely separated in leg 3 and leg 4. Leg 5 (fig. 19) uniramous, very rudimentary, 10 by 9 μ; located at junction of "tail" and trunk and armed with three long setae. Leg 6 absent.

Immature adult female.—Body (figs. 21-23) noncyclopid, shaped differently in different stages of metamorphosis; proportions of various body regions also different in different stages (see table 2).

Table 2.—*Measurements of immature adult females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico.*

Specimen number	Head	Neck	Trunk	"Tail"	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.28 by 0.44	0.08	0.47 by 0.47	0.17 by 0.24	0.96
2	.36 by 0.49	.09	.45 by 0.49	.17 by 0.23	1.07
3	.34 by 0.49	.10	.51 by 0.57	.17 by 0.27	1.12
4	.31 by 0.49	.10	.74 by 0.56	.17 by 0.25	1.13
5	.33 by 0.52	.10	.70 by 0.54	.18 by 0.24	1.23
6	.30 by 0.47	.11	.82 by 0.60	.17 by 0.23	1.31
7	.34 by 0.55	.10	.73 by 0.56	.18 by 0.23	1.33
8	.34 by 0.57	.09	.75 by 0.60	.17 by 0.26	1.35
9	.31 by 0.56	.11	.85 by 0.86	.16 by 0.25	1.43
Average	0.32 by 0.51	0.10	0.67 by 0.64	0.17 by 0.25	1.21

Structure of appendages similar to mature ovigerous female. Details of these immature adult females are given in following section in discussion of metamorphosis.

Female copepodid.—Body (fig. 20) cyclopoid, 0.70 by 0.37 mm. (excluding setae on caudal rami); no segmentation on cephalothorax and urosome, but with clear distinction between each two adjoining regions of four body regions. Cephalothorax semicircular anteriorly and rather truncated posteriorly; posterior surface roughly separated into dorsal and ventral portions. Second pedigerous segment (= neck of adult), 0.08 by 0.26 mm., attached to center of posterior surface of cephalothorax, carrying leg 2 ventrally at anterior margin. Third pedigerous segment, 0.13 by 0.26 mm., slightly invaginated on both sides and incompletely separated from fourth pedigerous segment on dorsal surface. Fourth pedigerous segment, 0.12 by 0.26 mm., with posterior margin protruding over about one-third of urosome. Urosome (= "tail" of adult) 0.17 by 0.23 mm., carrying inside a pair of seminal receptacles (or cement glands ?). Egg sac attachment area similar to that in adult.

Caudal ramus attached to posteroventral surface of urosome, its armature as in adult. Two sclerites on dorsal surface of third and fourth pedigerous segment. Micropits present on body surface (omitted in fig. 20).

All appendages similar to those in adult ovigerous female and immature adult female.

Remarks

In the vial labeled Cat. No. 38619 in the collection of USNM are two specimens (one decapitated) designated by Wilson (1911) as the type specimens of *Tucca corpulentus.* The trunk of the headless specimen appears like the one shown in fig. 24, namely, squarish and distinctly 3-lobed on its posterodorsal surface. The head of this specimen was supposedly dissected by Wilson for study of the mouth parts and other cephalic appendages, and probably was the source of his figs. 122–125. The other specimen (with head) is, doubtlessly, the source of his fig. 121. I have examined the latter specimen with great care in lactic acid. Nevertheless, I was not able to find any appendages that are significantly different from those described above. In addition, the posterodorsal surface of the trunk is also 3-lobed, not as smooth as illustrated by Wilson in his fig. 121. The circular appearance of this specimen is possibly due to the fact that the parasite was somewhat pressed (by the fin, on which the parasite was attached, pressing against the body surface) before preservation, because its trunk appears unusually thin. The absence of pits or impressions on body surface, one of the characters cited by Wilson for establishing the new species, is conceivably also due to mechanical deformation prior to preservation.

Consequently, as far as these two type specimens are concerned, *T. corpulentus* does not differ from *T. impressus* and should be synonymized with it. There are some inconsistencies between the label of Cat. No. 38619 in the USNM and the statement of Wilson (1911: 359): "There is but a single lot of this species, which was taken from the northern swell-toad, *Spheroides maculatus,* at Woods Hole, Massachusetts, and is numbered 38619, U.S.N.M. It includes three females, two of which bear egg-strings." The label of Cat. No. 38619 clearly says, however, that there are only "2 ♀ specimens," the host is "*Chilomycterus geometricus,*" and no egg strings were found in the vial. Another USNM collection of *T. corpulentus* is Cat. No. 79595. The label of this collection fits better with Wilson's statement. It says that there are "3 specimens" and the host is "Gills, *Spheroides maculatus,*" but the three specimens of this collection are *Pseudochondracanthus diceraus* Wilson. They are mature adult females and all carry a pygmy male on their posteroventral surface. This collection was not mentioned by Wilson in any of his reports, not even in his reports of *P. diceraus* (1908: 436; 1932: 496), but the label says "Identified by C. B. Wilson." I have taken the two specimens kept in the vial of Cat. No. 38619 as Wilson's type specimens of *T. corpulentus* and synonymized the species with *T. impressus.*

One of the three immature adult females in the vial of Cat. No. 38625 was obviously mistaken by Wilson for an adult male. The rather small size, the different shape and proportion of various body regions, and the two bean-shaped reproductive organs inside the urosome might suggest incorrectly a male, if the process of metamorphosis in the female is unknown. The pair of stout hooks described by Wilson on the ventral surface at the posterior corners of the genital segment of this "male" specimen are merely two sclerotic protrusions (see fig. 3).

NOTES ON METAMORPHOSIS

The absence of the male parasites on the diodontid and tetraodontid fishes perhaps occurs because males do not grow beyond the copepodid stage. They probably die after copulation as do the males in the families Lernaeidae, Lernaeoceridae, and Pennellidae, in which only the female copepodid (after copulation) attaches to the fish host and metamorphoses into an adult.

The two youngest females recovered from the diodontid fish caught off Cape San Blas, Fla., still show a cyclopoid form of body; they are particularly reminiscent of bomolochid and taeniacanthid copepods (see fig. 20). The cephalothorax is the widest part of the body, and the metasomal segments are still distinguishable (see table 3 for measurements). These features, in comparison with the metamorphosed adult female, indicate that they are either still in the last copepodid stage or, at most, just on the way to metamorphosis. The somewhat older females that I have in the same collection are the nine copepods that show no segmentation in the metasomal region, have swollen trunks as wide as the head or a little wider, and carry no egg sacs (see figs. 21, 22).

TABLE 3.—*Measurements of female copepodid from three collections.*

Record and body part measured	Specimen 1	Specimen 2	Specimen 3	Specimen 4
Host	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus antennatus*
Locality	Panacea, Fla.	Cape San Blas, Fla.	Cape San Blas, Fla.	Montego Bay, Jamaica
Date	May 14, 1965	May 16, 1965	May 16, 1965	June 15, 1910
Cephalothorax (head)	0.27 by 0.37	0.31 by 0.41	0.30 by 0.42	0.31 by 0.47
Thorax (neck +trunk)	.30 by 0.26	.34 by 0.32	.36 by 0.31	.41 by 0.37
Urosome ("tail")	.17 by 0.23	.16 by 0.23	.17 by 0.21	.15 by 0.23
Total length	.70	.81	.83	.86

These females I have considered as the immature adults inasmuch as they have attained sexual maturity and have copulated but have not yet produced egg sacs.

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome. As far as the size and shape are concerned, the second pedigerous segment and the urosome in the copepodid are not significantly different from the neck and the "tail" in the immature adult female, nor in the ovigerous female. The second thoracic segment, urosome, and all appendages are not transformed during metamorphosis, but the cephalothorax and the third and fourth pedigerous segment are tremendously changed.

The size of the head of an immature adult female (0.32 by 0.51 mm.) is not much different from that of the cephalothorax in the copepodid (0.31 by 0.42 mm.); the shape, however, is markedly different. The expansion is seen mostly in anterior corners, posterior subcorners, and the dorsal surface of the head. The head of an ovigerous female (0.33 by 0.59 mm.) differs from that of the immature adult female chiefly in the more globular appearance of the middorsal surface; it is not lengthened but definitely widened. The metamorphosis in the head involves changes in form from semicircular to rectangular (in dorsal view) and from slightly convex to globular (in lateral view of the dorsal surface). The amount of increase in proportions of the head is about 10 percent in the length and 45 percent in the width; this widening rather then lengthening during metamorphosis is due to the formation of the lateral wings.

The second and third pedigerous segments are completely fused into a unit at the onset of metamorphosis (fig. 21). This fused trunk is then enlarged in three dimensions, the shape (in dorsal view) changes from oval (as in fig. 21) to guitar-shaped (as in fig. 22) or nearly circular (as in fig. 23) and then to squarish (as in fig. 1). The posterior lobes, three on the dorsal and two on the ventral surface, are not formed in the immature adult female. The four chitinized platelets on the dorsal surface of the thorax of the copepodid are retained throughout metamorphosis. As these platelets are the points of attachment of trunk muscles on the tergum of the second and third pedigerous segment, they have not been elevated by the enlarging action in the course of metamorphosis. Thus, the four platelets form the bottom of the "four pits" on the dorsal surface of the ovigerous female. The amount of increase in proportions of the trunk is about 270 percent in the length and 120 percent in the width. The metamorphosis of the trunk, contrary to that of the head, involves more lengthening than widening.

Specimens 4, 5, 6, 7, and 8 of table 2 have trunks distinctly longer than wide; they look like that in fig. 22. The remaining four specimens (1, 2, 3, and 9) of the immature adult females in the same collection have trunks nearly as long as wide and resemble fig. 23. In the present state of knowledge, we can say only that immature adult females have two forms. Which form comes first in the process of metamorphosis is unknown.

A comparison between table 2 and table 4 shows that the maturity of the females can be judged by the size of the trunk, in addition to the presence or absence of egg sacs. The trunk is definitely longer and wider in ovigerous females than in immature adults, although the size of the head overlaps broadly in the two stages.

The first ovigerous female in table 4 has smaller body length, but a definitely larger trunk, than the largest immature adult female in table 2. As noted in the previous section, the neck of this ovigerous female is unusually shrunken; therefore, body length alone is not a good measure for determining the maturity of a female.

GEOGRAPHICAL VARIATION

According to our present knowledge of parasitic copepods of fishes, *Tucca impressus* is parasitic exclusively on two families of fishes, Tetraodontidae and Diodontidae—especially the fishes of the latter family (porcupine fish or boxfish). Our past records show that it is most abundant on the fishes of the genus *Chilomycterus* (Diodontidae) and always found either on the fins or on the body surface.

A certain degree of variation is observed in the head and the trunk of the ovigerous females collected from three different areas, namely the west coast of North Atlantic Ocean, the Gulf of

TABLE 4.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.29 by 0.50	0.06	1.30 by 0.95	0.17 by 0.24	0.84	1.38
2	.30 by 0.61	.11	1.10 by 1.22	.16 by 0.23	1.29	1.51
3	.33 by 0.55	.09	1.12 by 0.93	.17 by 0.25	.75	1.54
4	.31 by 0.56	.09	1.19 by 1.02	.18 by 0.23	1.10	1.59
5	.31 by 0.64	.09	1.14 by 0.87	.19 by 0.26	broken	1.68
6	.30 by 0.60	.08	1.33 by 1.12	.18 by 0.26	broken	1.71
7	.35 by 0.56	.10	1.30 by 1.40	.18 by 0.25	1.34	1.75
8	.36 by 0.65	.09	1.31 by 1.31	.18 by 0.24	1.84	1.77
9	.38 by 0.59	.11	1.28 by 1.48	.16 by 0.25	broken	1.78
10	.33 by 0.65	.10	1.59 by 1.14	.18 by 0.26	1.41	2.02
Average	0.33 by 0.59	0.09	1.24 by 1.17	0.17 by 0.25		1.67

TABLE 5. *Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *at Morehead City, North Carolina (from USNM 47748)*[1]

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.38 by 0.67	0.10	1.76 by 1.65	0.18 by 0.24	(2.79)	2.24
2	.30 by 0.78	.09	2.02 by 1.60	.17 by 0.23	-------	2.47
3	.35 by 0.96	.08	2.15 by 2.06	.19 by 0.24	-------	2.63
4	.37 by 0.91	.12	2.30 by 1.79	.16 by 0.25	-------	2.79
5	.31 by 0.84	.13	2.29 by 1.89	.16 by 0.26	-------	2.80
6	.34 by 0.88	.11	2.50 by 1.98	.16 by 0.24	-------	2.90
7	.36 by 0.85	.12	2.39 by 1.95	.17 by 0.27	-------	2.97
8	.37 by 0.91	.09	2.51 by 1.86	.18 by 0.26	-------	2.98
9	.38 by 0.94	.11	2.49 by 2.42	.19 by 0.27	-------	3.09
10	.40 by 0.89	.12	2.46 by 1.95	.17 by 0.25	(4.61)	3.16
Average	0.36 by 0.86	0.11	2.39 by 1.92	0.17 by 0.25	-------	2.80

[1] The egg sacs were found free in the vial. Since there is no way to identify each sac with its female, only the shortest and the longest sacs were measured.

TABLE 6.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus antennatus *at Montego Bay, Jamaica (from USNM 42273)*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.31 by 0.48	0.11	0.93 by 0.83	0.17 by 0.26	0.68	1.42
2	.32 by 0.54	.09	.96 by 0.78	.19 by 0.27	broken	1.46
3	.33 by 0.60	.09	1.15 by 1.13	.18 by 0.25	1.02	1.59
4	.35 by 0.56	.10	1.29 by 1.10	.16 by 0.27	1.77	1.75
5	.34 by 0.58	.08	1.42 by 1.22	.18 by 0.26	broken	1.78
6	.35 by 0.59	.11	1.35 by 1.29	.16 by 0.23	1.59	1.81
7	.34 by 0.56	.12	1.41 by 1.26	.15 by 0.24	2.05	1.83
8	.33 by 0.66	.09	1.47 by 1.27	.18 by 0.26	2.14	1.95
9	.36 by 0.66	.10	1.46 by 1.36	.18 by 0.25	broken	2.00
10	.34 by 0.68	.11	1.67 by 1.41	.17 by 0.26	broken	2.14
Average	0.34 by 0.59	0.10	1.31 by 1.17	0.17 by 0.26	-------	1.77

Mexico, and the Caribbean Sea. This variation occurs only in the metamorphosed parts of the body, and is in the size and the shape. A comparison of fig. 1 (a representative from the Gulf of Mexico), fig. 24 (a representative from the west coast of North Atlantic Ocean), and fig. 26 (a representative from the Caribbean Sea) together with reference to tables 4, 5, and 6 shows this picture of geographical variation. In the following discussion, for the sake of convenience, the specimens from Georgia, North Carolina, and Massachusetts are termed as the Atlantic type; the specimens from Florida (west coast), Mississippi, and Louisiana, the Gulf type; and the specimens from Jamaica, the Caribbean type.

The bilobed condition of the lateral wings of the head is generally most pronounced in the Caribbean type (figs. 26, 27), but the wings are almost unlobed in the Gulf type (fig. 1). The lateral wing of the Atlantic type (fig. 24) is only slightly bilobed; the posterior lobe is larger than the anterior lobe and is wider than those in the other two geographical types.

In both Gulf type and Atlantic type, the posterior lobes in the trunk are usually less pronounced, and there are no anterior lobes. These anterior and posterior lobes are, however, present and well formed in the Caribbean type. A fully grown ovigerous female of an Atlantic type is much larger than those of the Gulf type and the Caribbean type. The following data were derived by considering all collections from a general geographical region as a whole to show the size ranges (in millimeters) of the ovigerous females of the three different geographical types:

	Caribbean type	Gulf type	Atlantic type
	Mm.	*Mm.*	*Mm.*
Smallest	1.36 (in USNM 42251)	1.51 (off Cape San Blas, Fla.)	1.59 (in USNM 38625)
Largest	2.14 (in USNM 42273)	2.51 (Carrabelle, Fla.)	3.16 (in USNM 47748)
Longest egg sac	2.78	4.09	4.61

Thus, the shape of the trunk indicates that the Gulf type is closer to the Atlantic type than to the Caribbean type, but the size of the trunk indicates that the Gulf type is, on the contrary, closer to the Caribbean type than to the Atlantic type. In other words, comparisons of the trunk show that the Gulf type is intermediate between the Atlantic type and the Caribbean type. The variation of the head, in the Atlantic type, instead of the Gulf type, shows the intermediate character in the bilobed condition of the lateral wings.

I have found specimens in USNM collections (Cat. No. 38625 and 74375), from Beaufort, N.C., which, instead of having the Atlantic type trunk, have the posterior lobes of the trunk fairly well defined as in the Caribbean type. Moreover, in the collections from Jamaica, some individuals lack the anterior lobes in the trunk, as shown in fig. 27. It appears, therefore, that the variation in the head and the trunk is not absolute, or, in other words, that this variation is merely a general tendency of modification that exists in a certain geographical area but is not strictly expressed by every individual of this species found in a given geographical range. As the hosts of this parasitic copepod are mostly inshore fishes and not powerful swimmers, considerable distant movement probably is accomplished only by drifting with the current. At present, however, it is impossible to determine whether the Gulf Stream has influenced this picture of geographical variation.

The single specimen of *T. impressus* described by Krøyer (1837) is a female taken from the inner surface of the pectoral fin of a *Diodon hystrix* in the Danish West Indies. It definitely belongs to the Caribbean type, since in Krøyer's fig. 2a (dorsal view) and fig. 2b (lateral view) the posterior lobes, anterior lobes, and the bilobed condition in the head are of that type. According to Kroyer's description (p. 479) this Danish West Indian specimen measures 2 lines, of which the egg sac is about half. In other words, the length of the parasite's body is about 2.11 mm., which falls within the range of the Caribbean type (see table 6).

The 37 specimens of *T. impressus* described by Carvalho (1951) from Brazilian *C. schoepfi* measure from 1.52 to 1.80 mm., and so fall within the range of the Caribbean type.

In his discussion of the validity of Nordmann's *T. impressus,* Wilson (1911: 359) expressed his doubt upon the variation of the specimens of *T. impressus:* "either Nordmann's species or that of the present author is new to science. They can not both be identical with Kroyer's *T. impressus.*" This implies that Wilson's specimens are different from Krøyer's *T. impressus* to a certain degree, but this difference is not as significant as the discrepancy between Krøyer's *T. impressus* and Nordmann's *T. impressus.* Consequently, Wilson identified his specimens collected in Beaufort, N.C., as *T. impressus,* and created *T. verrucosus* for Nordmann's *T. impressus.*

The total length (1.67 mm.) given by Wilson (1911: 356) for the species of *T. impressus* is too small for the Atlantic type. I have measured all 30 specimens that were identified by Wilson as *T. impressus* in USNM collections. The collections, number of specimens, and maximum sizes are:

Catalogue number	Number of specimens	Smallest (*mm.*)	Largest (*mm.*)
USNM 38625..	11 (3 immature)	1.13	1.69
USNM 38627..	8	2.04	2.23
USNM 38628..	11	1.86	2.49

It is obvious, therefore, that Wilson took into consideration only the specimens in USNM 38625. This collection unfortunately contains no fully grown ovigerous females (judged by the length of the egg sac). One of the three immature adult females in this collection was described by Wilson as a male, and the measurements given for it are (Wilson, 1911: 357):

Total length, 1.27 mm.; cephalothorax, 0.3 by 0.5 mm.; trunk 0.75 by 0.51 mm.; and width of genital segment, 0.25 mm.

These figures lie within the range of the immature adult female with a longer (guitar-shaped) trunk given in table 2.

The 10 specimens of *T. impressus* reported by Nordmann (1864) were taken from a "fleckigen Diodon–Art." According to Nordmann's description on p. 491, these parasites measure about 5 mm. long including the egg sac. Judging from his illustration of a complete parasite in pl. VI, fig. 7, the body is about 3.15 mm. long and the egg sac, 1.85 mm.; therefore, the size is about that of the Atlantic type of the *T. impressus.* According to what Nordmann described (pp. 491–494) and illustrated (pl. VI, figs. 7–10), however, this West African species of *Tucca* is definitely different from all three types of *T. impressus* in the North and South American waters.

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MORPHOLOGY AND DISTRIBUTION OF LARVAL WAHOO *ACANTHOCYBIUM SOLANDRI* (CUVIER) IN THE CENTRAL PACIFIC OCEAN

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ABSTRACT

Descriptions are presented of the early developmental stages of the wahoo, *Acanthocybium solandri* (Cuvier), ranging from 2.8 to 23.7 mm. in standard length. Developmental changes in body pigmentation, body form, fin formation, and ossification of bones and other hard parts were studied for 38 larvae collected in the central Pacific Ocean. Drawings of larvae at various sizes are included. Certain adult characters are discussed, such as: the number of vertebrae and the vertebral formula; the number of spines and rays in the first dorsal, second dorsal, and anal fins; and the number of dorsal and anal finlets.

Larval and adult wahoo live in the open ocean as well as near land. The adults spawn throughout the tropical and subtropical waters between lat. 30° N. and 25° S. The species spawns throughout the year in the equatorial waters between lat. 14° N. and 15° S., and during the northern and southern summer in areas farther from the Equator.

Although considerable knowledge has been gained in recent years about the early life history of the commercially important mackerels and tunas, the larval and juvenile stages of many scombroid fishes are poorly known. This is particularly true of the larvae of the wahoo, *Acanthocybium solandri* (Cuvier). The smallest wahoo previously recorded was a 23.7-mm. juvenile from the central Pacific Ocean (Strasburg, 1964). Prior to this record, the only mention of a young wahoo in the literature was a 28-cm. juvenile caught off Japan in 1917 (Kishinouye, 1923).

The wahoo, a member of the Scombridae, is usually taken in small quantities as incidental catches on the longline, and in larger quantities by surface trolling (Iversen and Yoshida, 1957). It is found in tropical and subtropical areas of the oceans.

While sampling for tuna larvae in the central Pacific Ocean from 1950 to 1962, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, collected 38 young wahoo from 2.8 to 17.8 mm. SL (standard length) in plankton net hauls. The morphology and distribution of the larvae were studied to increase our knowledge of the early life history of the scombroid fishes.

This paper describes the developmental changes in body pigmentation, fin formation, and ossification of various bones. It also discusses certain adult characters that require definition, such as the number of vertebrae and the vertebral formula, the number of spines and rays in the dorsal and anal fins, and the number of finlets. The growth rates of various body parts are included, as well as new information on distribution of the species in the central Pacific Ocean, as determined from captures of the larvae and adults.

COLLECTION AND TREATMENT OF MATERIAL

Plankton hauls were made with a 1-m. plankton net on 32 cruises of the Bureau of Commercial Fisheries research vessels *Hugh M. Smith* and *Charles H. Gilbert* from May 1950 to July 1962. The types of hauls varied slightly over the years; generally, the net was hauled obliquely from a depth of 200 m. to the surface before 1956, but from 1956 to 1962, it was

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hauled obliquely from 140 m. to the surface. On a few cruises the net was hauled obliquely from a depth of 60 m. and horizontally near the surface. Each haul lasted 30 minutes.

Of the 1,643 plankton samples obtained, 600 were taken near the Hawaiian Islands (lat. 15° to 30° N., long. 150° to 165° W.) and most of the others in the equatorial region (lat. 10° N. to 10° S., long. 110° to 170° W.). The 38 wahoo larvae were found in 34 plankton samples; 2 larvae were found in two samples and 3 larvae in one (fig. 1 and table 1). All the larvae were preserved in a 10 percent solution of Formalin.[1] The wahoo larvae ranged from 2.8 to 17.8 mm. SL. The size range was extended to 23.7 mm. by the inclusion of a juvenile (collected in a midwater trawl) described by Strasburg (1964).

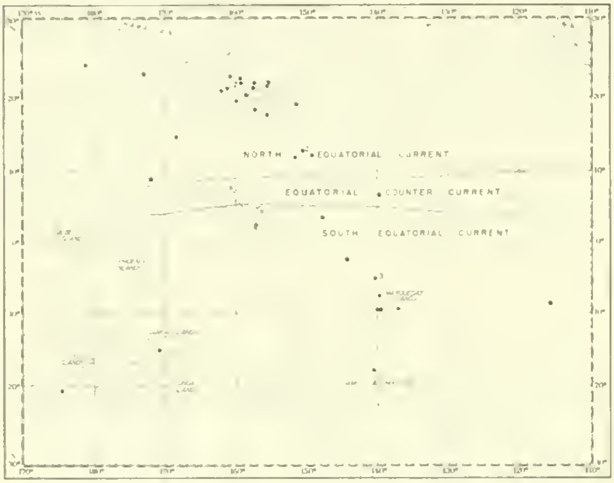

FIGURE 1.—Locations at which wahoo larvae were taken in plankton net hauls. Each star represents a single larva. A star and number show catches of two or more larvae. Broken lines indicate a distance of 110 kilometers from land. Major currents of the central Pacific Ocean are shown.

Of the 38 larvae, 21 were cleared in a weak (1–2 percent) solution of potassium hydroxide and stained with alizarin in the technique described by Lipman (1935). Standard length and various body parts were measured, and counts of fin rays and spines, myomeres, teeth, and branchiostegal rays were made before clearing and rechecked after staining. Vertebrae were counted after the specimens had been stained. In a few instances where the body was slightly bent, a small piece of glass slide was placed over the specimen to straighten it before measuring. The following measurements were made on each specimen:

TABLE 1.—*Record of larval and juvenile wahoo captured in plankton net hauls in the central Pacific Ocean, 1950–62*

Limits of latitude and date	Cruise	Position		Local time	Surface temperature	Distance from land	Standard length
Lat. 15° 30° N.		*Lat.*	*Long.*		*° C.*	*Km.*	*Mm.*
May 17, 1950	HMS-4[1]	21°06′ N.	161°06′ W.	0925	24.6	139	3.4
May 18, 1950	HMS-4	19°25′ N.	159°50′ W.	1048	24.8	185	4.1
May 24, 1950	HMS-4	21°53′ N.	159°09′ W.	0120	22.8	93	2.8; 4.2
June 17, 1954	HMS-26	20°51′ N.	161°59′ W.	0512	25.9	222	3.1
July 1, 1950	HMS-5	22°58′ N.	173°00′ W.	2312	26.1	333	7.4
July 12, 1962	CHG-58[1]	22°44′ N.	160°47′ W.	0100	25.5	139	5.8
July 22, 1951	HMS-10	22°27′ N.	159°15′ W.	0715	25.6	37	4.8
July 30, 1951	HMS-10	21°25′ N.	155°30′ W.	1343	25.5	110	4.3
Aug. 5, 1953	HMS-21	21°10′ N.	157°28′ W.	0240	25.4	28	5.5
Aug. 7, 1953	HMS-21	21°53′ N.	155°21′ W.	0315	24.8	157	3.8
Aug. 16, 1960	CHG-48	24°15′ N.	178°54′ E.	1800	26.7	592	8.7
Aug. 19, 1950	HMS-6	20°15′ N.	158°24′ W.	2340	26.7	130	8.4
Aug. 21, 1953	HMS-21	17°40′ N.	155°30′ W.	0120	25.0	130	4.6
Aug. 21, 1953	HMS-21	18°14′ N.	157°09′ W.	2038	25.8	148	4.3
Sept. 10, 1952	HMS-17	21°48′ N.	157°18′ W.	1149	25.2	37	4.4
Oct. 4, 1951	HMS-11	19°00′ N.	151°19′ W.	0750	25.4	389	5.7
Lat. 14° N - 14° S.							
Jan. 12, 1959	HMS-50	12°42′ N.	150°24′ W.	2006	26.1	890	7.6; [2] 7.9
Feb. 9, 1958	HMS-43	7°35′ S.	139°40′ W.	2110	28.5	46	7.8
Mar. 13, 1954	CHG-15	8°42′ S.	115°39′ W.	1954	26.4	2,057	5.8
Mar. 16, 1956	HMS-33	5°03′ S.	140°16′ W.	1949	26.3	315	5.2; 6.2 [2] 6.6
Apr. 16, 1954	CHG-15	2°09′ N.	157°05′ W.	1932	27.7	28	4.3
Apr. 23, 1958	CHG-38	2°34′ S.	144°12′ W.	2003	28.4	732	17.8
Apr. 25, 1958	CHG-38	3°15′ N.	147°40′ W.	2003	28.6	1,047	9.0
May 29, 1952	HMS-15	6°36′ N.	139°44′ W.	1035	27.7	1,556	6.6
June 10, 1954	HMS-26	14°33′ N.	168°25′ W.	1739	26.6	232	10.7
June 19, 1958	HMS-45	12°02′ N.	149°03′ W.	2010	27.0	1,055	5.9
July 6, 1950	HMS-5	8°54′ N.	172°00′ W.	2012	26.9	912	4.5
Aug. 30, 1956	CHG-30	9°22′ S.	137°01′ W.	2000	25.2	167	9.2
Oct. 6, 1957	CHG-35	11°42′ N.	151°30′ W.	0000	27.6	908	5.2
Dec. 1, 1957	CHG-35	9°33′ S.	139°51′ W.	0839	27.5	56	10.2
Dec. 1, 1957	CHG-35	9°34′ S.	139°50′ W.	1406	28.6	56	3.9
Lat. 15° 25° S.							
Feb. 14, 1962	CHG-55	20°34′ S.	175°29′ E.	2004	27.0	145	13.2
Mar. 5, 1957	HMS-38	17°56′ S.	140°28′ W.	2030	28.1	28	2.8
Mar. 13, 1962	CHG-55	15°05′ S.	170°48′ W.	2000	27.9	56	6.8

[1] Bureau of Commercial Fisheries research vessels, *Hugh M. Smith* (HMS) and *Charles H. Gilbert* (CHG).
[2] Length of 7.9-mm. and 6.6-mm. specimens estimated

Standard length: The distance from anteriormost tip of snout to posterior end of notochord; after the notochord had flexed dorsad, the distance from tip of snout to posterior edge of hypural complex was measured.

Head length: The distance from anteriormost tip of snout to dorsal end of gill cover.

Snout length: The distance from anteriormost tip of premaxillary to anterior edge of orbit.

Orbit diameter: The greatest distance measured along the longitudinal axis of the body.

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

This measurement was chosen over eye diameter because the eyes tend to shrink in preservative, and some had been lost.

Premaxillary length: The distance from tip to anterior edge of the mesethmoid, measured along the dorsal profile of the snout.

Upper and lower jaw lengths: The distance from anteriormost tip to posterior edge of maxillary and mandible.

Body depth: Vertical distance immediately behind the anus.

Snout to anus distance: The straight-line distance from anteriormost tip of snout to posterior edge of anal opening.

Snout to first and second dorsal fins: the straight-line distance from anteriormost tip of snout to origins of the fins.

DEFINITION OF CERTAIN ADULT CHARACTERS

In the identification of larval and juvenile fishes, it is important that the adult characters be defined accurately because they are often applicable to the young as well. One useful skeletal character for the diagnosis of adult scrombrids is the number of vertebrae. Previous literature on the wahoo contains a wide variation in vertebral number, which is unusual in the family Scombridae. The number of vertebrae among most scombrids is known to be nearly constant (Ford, 1937; Godsil and Byers, 1944; Clothier, 1950), but a number of reports with descriptions of wahoo (table 2) give the vertebral formula as 23 to 33 + 31 to 34 = 54 to 66 (precaudal vertebrae + caudal vertebrae = total vertebrae).

I found that all papers published after 1923 which contained the formula 23 to 33 + 31 to 34 = 54 to 66 included Kishinouye (1923) as a reference. Kishinouye (1908, 1915, 1923) did not, however, discuss the wide range in number of precaudal vertebrae, or refer to the seemingly low count of 23 precaudals. It seems likely that the 23 first reported by Kishinouye (1923) is a typographical error and that 32 is the correct number.

Other evidence supports my suspicion that the reported low count of 23 precaudal verte-

TABLE 2.—*Counts of some meristic characters of wahoo*

Source	Length [1]	First dorsal spines	Second dorsal fin			Anal fin			Vertebrae		
			Rays	Finlets	Total	Rays	Finlets	Total	Precaudal	Caudal	Total
From literature	*Mm.*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Cuvier and Valenciennes (1831)		26	11	9	20	12	10	22			
Lay and Bennett (1839)		25		9½			9½				
Poey (1860)[2]	1,300 (FL)	25									
Doderlein (1872)[2]		26									
Jordan (1885)		24	I, 12	9	22	I, 12	9	22			
Jenkins (1904)		27	13	9	22	12	8	20			
Jordan and Evermann (1905)		25									
Kishinouye (1908)		26	11	10	21	11	9	20			65
Starks (1910)									32	34	66
Kishinouye (1915)		26	11	9	20	11	9	20	32 or 33	31	63–64
Kishinouye (1923)		26	11	9	20	11	9	20	32-33	31	[3] 63–64
Kishinouye (1923)	1,092 (FL)	26	11	9	20	11	9	20	33	31	[4] 64
Meek and Hildebrand (1923)	1,200 (FL)	26	12	9	21	11, 10	9	21			
Conrad and La Monte (1937)	1,468 (FL)										
Conrad (1938)		26							31	31	62
Morice (1953)		26		[4] 9			[4] 9				64
Strasburg (1964)	23.7 (SL)	27			24			23	32	31	63
Specimens examined by present author											
Longline fishing	1,435 (FL)	27	12	9	21	13	9	22	32	33	65
Do	1,554 (FL)	27	13	9	22	12	9	21	31	32	63
Do	1,252 (FL)	27	12	[5] 9(10)	21	12	[5] 9(10)	21	32	31	63
Do	1,066 (FL)	27	12	[5] 9(10)	21	13	[5] 9(10)	22	32	31	63
Do	1,300 (FL)								32	30	62
Do	1,245 (FL)								32	31	63
Marlin stomach	159 (SL)								32	31	63
Do	152 (SL)								32	31	63
Skipjack stomach	117 (SL)								31	33	64
Plankton haul	17.8 (SL)	27			23			22	33	30	63
Do	13.2 (SL)	27			23			22	32	31	63

[1] FL (fork length); SL (standard length).

[2] From Lütken, 1880.

[3] Number of precaudal and total vertebrae as corrected.

[4] From figure.

[5] Last 2 finlets fused.

brae is erroneous. First, no other report in the literature shows a wahoo having between 23 and 31 precaudal vertebrae, as one would expect if these counts encompassed the actual range of variation; instead, the number of precaudal vertebrae has always been cited as 31, 32, or 33 when it was referable to a particular specimen. Second, I found that six adult wahoo taken during a cruise of the *Charles H. Gilbert* to the southwestern Pacific in 1963 had either 31 or 32 precaudal vertebrae and 30 to 33 caudal vertebrae (table 2). Six juvenile specimens from other sources had 31 to 33 precaudal and 30 to 33 caudal vertebrae.

Although the number of vertebrae may vary slightly more in wahoo than in tunas, the variation is less than Kishinouye (1923) reported. The vertebral formula for wahoo can be restated as 31 to 33 + 30 to 34 = 62 to 66; the most typical formula is 32 + 31 = 63.

Other adult characters that are useful for identifying young wahoo are the number of spines and rays in the dorsal and anal fins. Varying counts have been given for these characters, also. Different authors have reported 24 to 26 first dorsal spines, except Jenkins (1904) who reported 27 (table 2). Each of four adult wahoo that I examined had 27 first dorsal spines, but the last 2 were greatly reduced and were buried beneath the skin and muscle tissue. Although it was relatively easy to locate the 26th spine by probing, it was extremely difficult to locate the 27th even with careful dissection of skin and musculature. This difficulty may account for the generally lower spine counts reported previously for the first dorsal fin. Three juvenile wahoo that I examined, including the specimen previously reported by Strasburg (1964) as having 26 spines, also had 27 first dorsal spines. The last spine was extremely small and appeared almost to be the first spine in the second dorsal fin. The number of spines in the first dorsal fin of the wahoo thus appears to be constant at 27.

The number of rays seems to vary slightly in the second dorsal (12 to 14) and anal fins (12 to 13). The counts of 11 rays for both fins in all of Kishinouye's reports and 11 rays for the second dorsal fin reported in Cuvier and Valenciennes (1831: table 2) may be too low (by error), or may represent extreme variations.

In adult wahoo the dorsal and anal finlets appear to be constant at 9, although Robert H. Gibbs, Jr. (personal communication) found the number to vary between 7 and 9 in 16 specimens he examined. While preparing the skeletal material for the present study, I observed that the posteriormost dorsal finlet and the posteriormost anal finlet, which appeared to be perfectly formed single finlets, were actually composed of two separate finlets that had become fused. The extra finlet is clearly reflected in the total ray and finlet counts of the three smallest wahoo (table 2). In both dorsal and anal series the number of elements is generally larger than the combined ray and finlet number of the adults.

DESCRIPTION AND DEVELOPMENT OF LARVAL AND JUVENILE WAHOO

Identification of wahoo larvae is simplified because it is a single species (Lütken, 1880; Jordan and Evermann, 1905; Beaufort and Chapman, 1951; Collette and Gibbs, 1963) and therefore the problem of differentiating morphologically similar species is eliminated. The larval characteristics described and illustrated in this paper were obtained from specimens that had been preserved in 10 percent Formalin for many years and were sometimes based on single specimens. The description, therefore, may differ slightly from that of newly caught specimens.

Larval wahoo less than 3.4 mm. SL are readily recognized by several characteristics: (1) the large number of body segments in relation to body length; (2) the elongate viscera; and (3) the presence of one or two black pigment spots on the ventral surface of the caudal peduncle, similar to those on larvae of skipjack tuna (*Katsuwonus pelamis*). Larvae as small as 2.8 mm. have 63 to 65 body segments, including the urostyle (compared with 42 to 43 segments in skipjack), and the viscera extend well over one-half the body length. Larvae above 4.4 mm. can be recognized by the large number of body segments, the extent of the viscera (over two-thirds the body length), and the length of the snout (more than twice the diameter of the orbit).

The development of the larval and early juvenile stages is discussed in the following sequence: (a) changes in pigmentation, (b) changes in body form, and (c) sequence of ossification. The term "larva" includes all specimens from the smallest to the juvenile stage, which starts at the time the full complement of spines and rays in all fins has ossified. In wahoo this point is reached before 23.7 mm. SL. The term "postlarva" is not used here. Standard length is the measure of body length, except when specified otherwise.

CHANGES IN PIGMENTATION

As is true for all fish larvae preserved in Formalin, the only pigment spots visible in wahoo larvae are the melanophores. Unlike larvae of *Trachurus* (Ahlstrom and Ball, 1954), Exocoetidae (personal observation), Istiophoridae (Ueyanagi, 1963), *Coryphaena* (Mito, 1960), and others, the wahoo larvae have comparatively few melanophores. Large changes in pigmentation as the larvae increase in size are seen only in four areas: (1) snout, (2) base of second dorsal fin, (3) base of anal fin, and (4) digestive tract (figs. 2 and 3). The following descriptions of pigmentation are based on the left side of the body as seen in lateral view.

Head Pigmentation

The midbrain area remains unpigmented in larvae smaller than 4.4 mm. (fig. 2A and B). The only exception was a 3.1-mm. larva which possessed a melanophore in this location. A single melanophore is present on the anterior portion of the midbrain in about half the larvae between 4.4 and 5.5 mm. (fig. 2A). Pigmentation in the anterior portion of the midbrain increases gradually with body length; 6 melanophores are present in the 10.7-mm. larva (fig. 3C), and about 27 in larvae up to 13.2 mm. long (fig. 3D).

Pigmentation appears on the forebrain much later than on the midbrain and the number of melanophores is small. A single melanophore appears on the forebrain in larvae about 7.4 mm. long, and the number of melanophores increases to only four or five in larvae up to 17.8 mm. long (specimen similar in appearance to that of figure 3D, except for heavier pigmentation).

Lateral pigmentation on the posterior portion of the head is completely lacking in larvae up to 13.2 mm. long, but about 50 small melanophores are present in the area posterior to the orbit and on the surface of the preopercle in larvae about 17.8 mm. long. In larvae of yellowfin tuna (*Thunnus albacares*) and skipjack tuna, some melanophores usually are present in the postorbital region in specimens shorter than 6.0 mm.

Pigmentation on the snout develops in two major areas: near the primordial nasal cavity and on the tip of the upper jaw. It is present on the snout in the smallest larva as a single small melanophore within the primordial nasal cavity and two or three melanophores on the tip of the upper jaw (fig. 2A). The pigmentation at the primordial nasal cavity develops slowly; additional melanophores are added within the cavity and on the surface of the snout anterior to it. As the nostrils form (when the larvae are between 10.7 and 13.2 mm. long), a few more melanophores appear on the surface of the snout between the anterior and posterior nostrils. The number of melanophores in this area is small, however, for no more than 13 to 15 are present in the 13.2-mm. larva (fig. 3D).

The number of melanophores increases slowly on the anterior portion of the upper jaw of larvae up to a length of about 4.3 mm.; however, above this size, as the upper and lower jaws begin to grow more rapidly in relation to body length, pigmentation on the anterior portion of the upper jaw increases noticeably. At a length of 6.8 mm. (fig. 3A), two or three rows of 18 to 25 melanophores are on the anterior part of the upper jaw. The number of melanophores increases with further growth of the fish, and the entire surface of the upper jaw anterior to the mesethmoid is covered in larvae larger than 13.2 mm. (fig. 3B-D). Additional melanophores develop posteriorly on the snout, and in the 17.8-mm. larva the pigmentation on the anterior portion of the upper jaw and around the nostrils has merged into a single, large pigmented area.

The tip of the lower jaw in larvae 2.8 mm. long has few melanophores, but the number

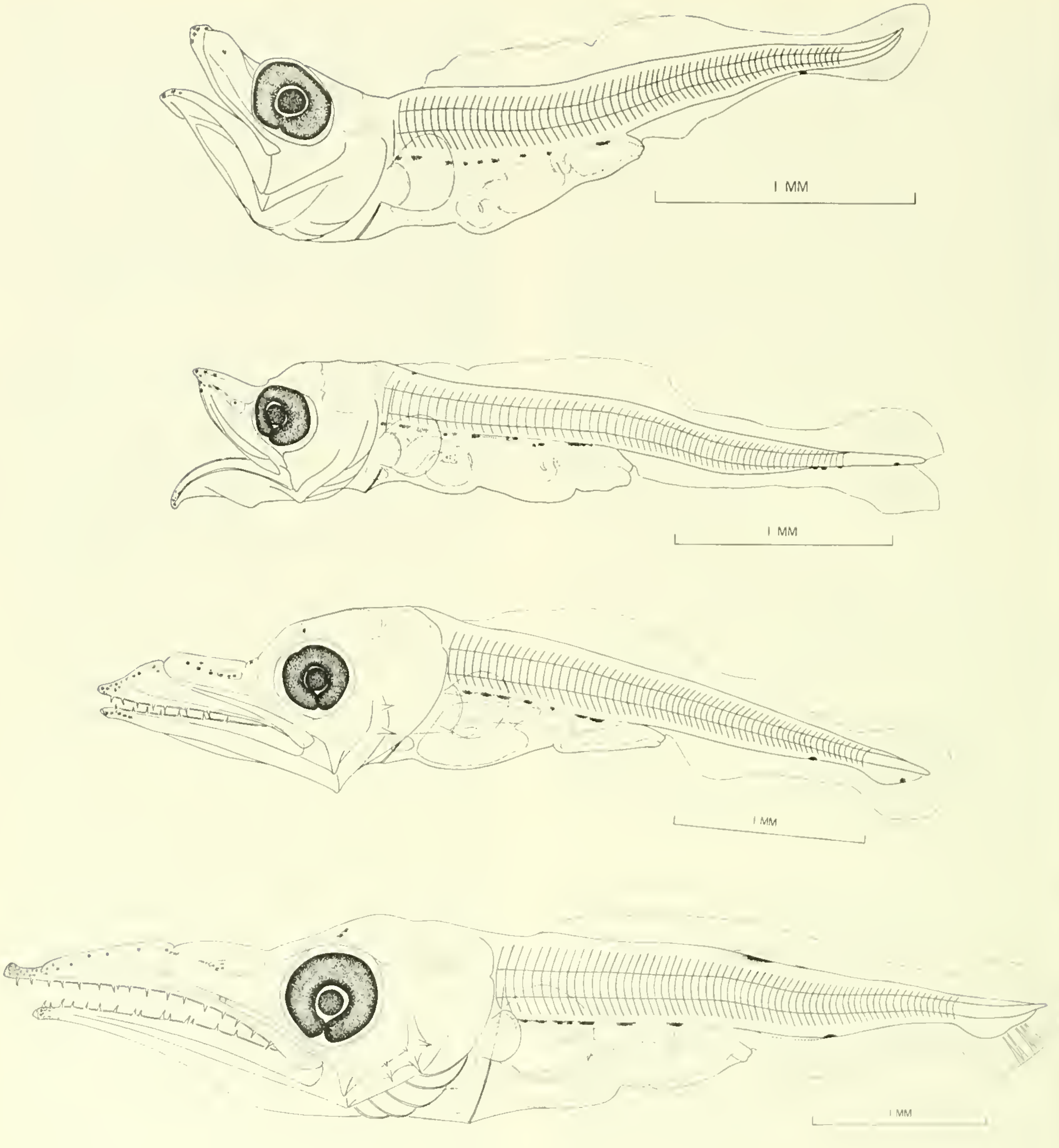

FIGURE 2.—Development of the larva of wahoo: A. larva, 2.8 mm. long; B. larva, 3.4 mm. long; C. larva, 4.4 mm. long; D. larva, 5.8 mm. long.

increases gradually to about seven or eight in the 8.4-mm. larva (fig. 3B). No melanophores appear on the conical cartilaginous projection at the tip of the jaw in larvae shorter than 5.8 mm., but some are present at lengths above 6.8 mm. In larvae over 10.7 mm., melanophores on the lower jaw are found only on the cartilaginous projection (fig. 3A-D).

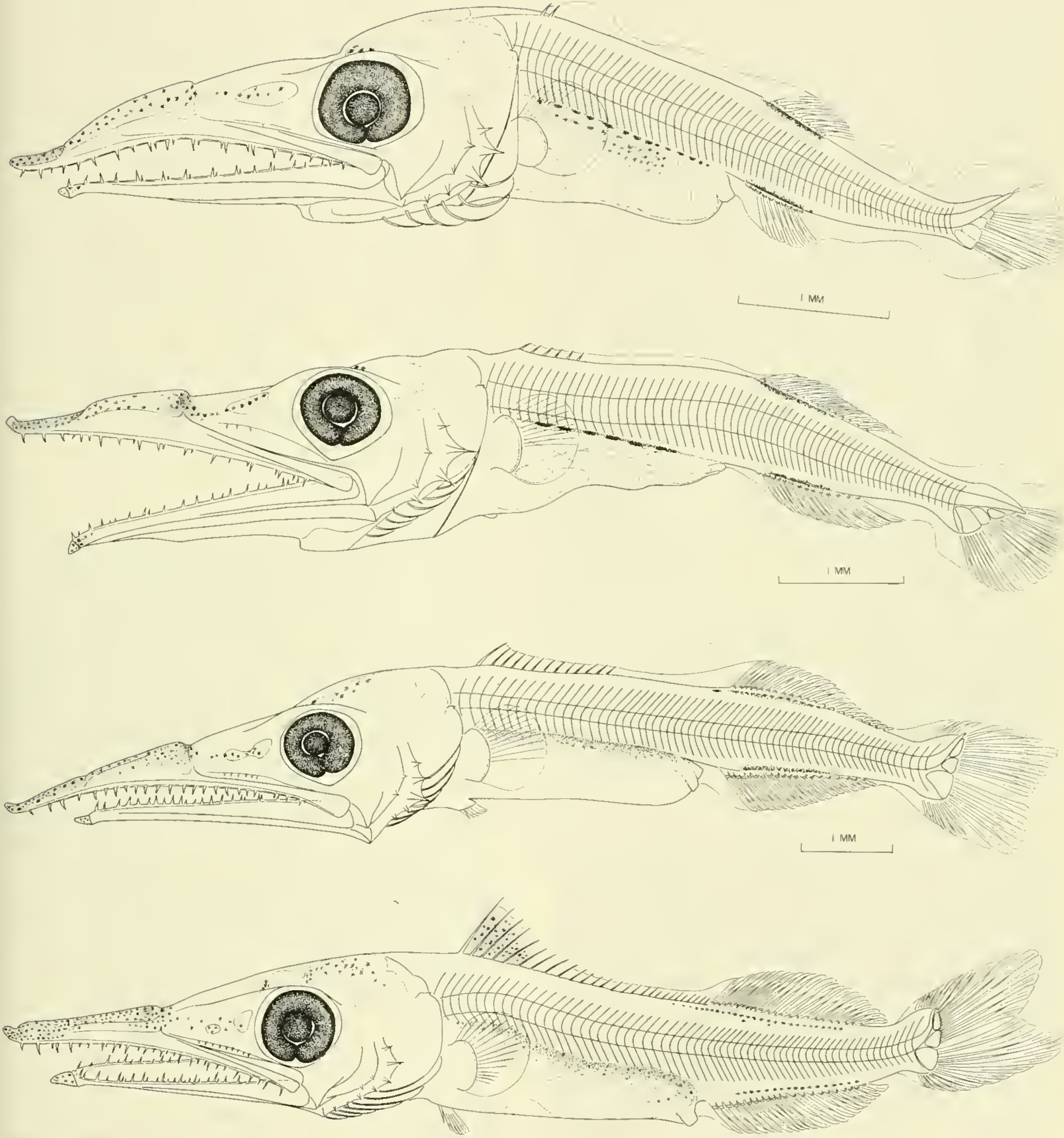

FIGURE 3.—Development of the larva of wahoo: A. larva, 6.8 mm. long; B. larva, 8.4 mm. long; C. larva, 10.7 mm. long; D. larva, 13.2 mm. long.

Preanal Trunk Pigmentation

The preanal trunk region is free of dermal pigmentation in larvae smaller than 10.7 mm.; the only pigmentation present is internal, along the dorsal part of the abdominal cavity. The pigmentation here consists of 7 to 10 large pigment spots, each composed of either a single melanophore or several small melanophores which are contiguous. These melanophores can be seen through the thin abdominal musculature in larvae smaller than 8.4 mm. (fig. 2A-D). The number of abdominal melanophores increases and they spread out ventrally over the peritoneum when the larvae are about 6.8 mm. long, but not in all larvae—see, for example, the 8.4-mm. larva of figure 3B. Evidently this spreading of melanophores varies among individuals. The abdominal melanophores of the 10.7-mm. larva have spread ventrally over the dorsal one-third of the digestive tract, and a few dermal melanophores have developed on the surface of the body over the dorsal part of the abdominal region (fig. 3C). Subsequently, only these dermal melanophores are noticeable, owing to a thickening of the abdominal musculature. Dermal pigmentation is lacking along the ventral surface of the body in the abdominal region. The 17.8-mm. larva has about 14 small dermal melanophores on the dorsal part of the first few myomeres, and a wide band of dermal melanophores over the lower half of the body posterior to the pectoral fin. This band extends to the level of the posterior end of the base of the anal fin.

Orton (1953) has shown that in certain teleost larvae, including two scombroids, *Pneumatophorus diego* and *Sarda lineolatus,* the pigment cells along the dorsal region of the body migrate ventrally and that in all pelagic species that she examined the first "wave" of pigment migration is typically completed in 2 days after hatching. In all except one wahoo larvae that I examined, the pigment spots were in a ventral position. One larva had a pigment spot at the nape (fig. 2B); possibly this was a melanophore that had not yet migrated ventrally.

Postanal Trunk Pigmentation

Two stages of pigment formation are evident in the postanal trunk area. The first is seen in larvae less than 4.4 mm. long, which usually have one but sometimes two or three melanophores on the ventral midline of the body near the caudal peduncle, and, in most specimens, a very small melanophore is near and ventral to the posterior end of the notochord (fig. 2A-D). These pigment spots resemble those in larvae of skipjack tuna. The second stage is seen in larvae 5.8 to 6.2 mm. long (fig. 2D); the melanophore at the caudal peduncle region has migrated anteriorly to the base of the anal fin and has increased in size. The 6.8-mm. larva has a group of fine granules of pigment that extend along the base of the anal fin (fig. 3A) in place of the enlarged melanophore; this pattern prevails until the larvae are more than 10.7 mm. long. In the 13.2-mm. larva, the granules of pigment are replaced by a series of evenly spaced melanophores that extend from about the middle of the anal fin to the base of about the eighth anal finlet (fig. 3D).

Fin Pigmentation

Fin pigmentation is not extensive, except on the first dorsal fin. Some fins, the pectoral, pelvic, and caudal, are unpigmented throughout the larval and early juvenile stages. Pigmentation on the first dorsal fin develops when the larvae are 10.7 to 13.2 mm. long. At 13.2 mm., at least the first five interspinous membranes of the first dorsal fin are pigmented with scattered melanophores of various sizes (fig. 3D), and at 17.8 mm., the first eight interspinous membranes are pigmented. In the 17.8-mm. larva, melanophores are also developed on the basal portion of nearly all dorsal and ventral finlets. When the juveniles are about 23.7 mm. long (see Strasburg, 1964: fig. 2), the basal half of the entire first dorsal fin and of all dorsal and ventral finlets is darkly pigmented.

CHANGES IN BODY PARTS

To study the growth of body parts, measurements (table 3) were made as described previously. Measurements of the larger body dimensions, such as standard length, head length, and distance from snout to anus and snout to second dorsal fin, were made to the

TABLE 3.—*Measurements of body parts of larval and juvenile wahoo*

Standard length [1]	Head length	Snout length	Orbit diameter	Premaxillary length [2]	Jaw length		Body depth	Distance snout to:			Pectoral fin length [3]	Pelvic fin length
					Upper	Lower		Anus	First dorsal fin	Second dorsal fin		
Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
2.8	0.8	0.24	0.26	0.05	---------	---------	0.20	1.8	---------	---------	(0.29)	---------
2.8	.8	.25	.26	.05	0.45	0.45	.20	1.8	---------	---------	(.31)	---------
3.1	.9	---------	---------	---------	---------	.49	.20	1.9	---------	---------	(.29)	---------
3.4	1.0	.33	.33	.05	.53	.53	.20	2.0	---------	---------	(.33)	---------
3.8	1.2	.47	.37	.08	.61	.61	.20	2.4	---------	---------	(.41)	---------
3.9	1.2	.49	.37	.10	.66	.66	.23	2.5	---------	---------	(.41)	---------
4.1	1.2	.49	.39	.10	.69	.69	.24	2.5	---------	---------	(.45)	---------
4.2	1.3	.52	.39	.15	.76	.76	---------	2.5	---------	---------	(.37)	---------
4.3	1.4	.53	.41	.17	.84	.84	.27	2.7	---------	---------	(.41)	---------
4.3	1.6	.74	.41	.27	.94	.94	.29	3.0	---------	---------	(.41)	---------
4.3	1.7	.78	.42	.27	.98	.98	.27	2.9	---------	---------	(.41)	---------
4.4	1.8	.87	.43	.33	1.09	1.03	.27	3.1	---------	---------	(.41)	---------
4.5	1.9	.90	.44	.38	1.15	1.07	.33	3.1	---------	---------	(.47)	---------
4.6	1.9	1.00	.47	.36	1.25	1.16	.38	3.1	---------	---------	(.49)	---------
4.8	2.1	1.10	.49	.49	1.41	1.28	.38	3.3	---------	---------	(.53)	---------
5.2	2.2	1.09	.51	.53	1.39	1.31	.43	3.4	---------	---------	(.49)	---------
5.2	2.3	1.25	.51	.68	1.52	1.39	.44	3.6	---------	---------	(.49)	---------
5.5	2.4	1.25	.54	.61	1.58	1.47	.41	3.8	---------	---------	(.49)	---------
5.7	2.6	1.31	.57	.74	1.63	1.50	.47	3.9	---------	---------	(.61)	---------
5.8	2.4	1.33	.57	.78	1.64	---------	.46	4.1	---------	---------	(.53)	---------
5.8	2.9	1.55	.57	.80	1.83	1.63	.49	4.3	---------	---------	(.59)	---------
5.9	2.7	1.52	.57	.86	1.84	1.64	.49	4.1	---------	---------	(.57)	---------
6.2	2.7	1.64	.57	.94	1.91	1.66	.49	4.3	3.4	4.3	(.53)	---------
6.6	3.3	1.93	.68	1.15	2.30	1.97	.55	4.9	3.5	4.8	.41	---------
6.8	3.3	1.89	.68	1.15	2.35	2.00	.56	4.9	3.7	5.1	.41	Bud
7.4	3.4	1.97	.74	1.23	2.30	1.95	.60	5.2	3.6	5.3	.44	Bud
7.6	3.4	2.01	.78	1.23	2.42	2.11	.64	5.3	3.8	5.4	.61	---------
7.8	3.6	2.13	.78	1.31	2.62	2.17	.64	5.5	3.9	5.5	.66	---------
8.4	3.8	2.46	.82	1.56	2.87	2.34	.70	6.0	4.2	6.3	.73	Bud
8.7	3.9	2.34	.82	1.56	2.85	2.30	.68	6.4	4.4	6.5	.78	Bud
9.0	4.0	2.38	.84	1.60	2.87	2.30	.70	6.4	4.4	6.5	.82	Bud
9.2	4.3	2.54	.90	1.68	3.07	2.46	.94	6.4	4.6	6.6	.82	0.16
10.2	4.9	3.03	1.03	1.97	3.65	2.95	1.07	7.6	5.4	7.8	.86	.10
10.7	4.9	3.07	1.09	2.01	3.77	3.07	1.12	7.7	5.5	8.1	.86	.29
13.2	6.4	3.57	1.40	2.25	4.43	3.69	1.48	9.9	6.7	10.0	1.35	.82
17.8	7.4	4.06	1.72	2.46	5.12	4.18	2.05	12.9	8.0	13.3	1.50	1.44
23.7	9.8	4.61	2.40	2.64	5.66	5.31	2.87	16.0	8.8	16.2	2.00	1.83

[1] Two badly damaged larvae (estimated lengths, 6.6 and 7.9 mm.) were not included in the series.
[2] The distance from tip to anterior edge of mesethmoid, measured along the dorsal profile of the snout.
[3] Length of larval pectoral fin in parentheses.

nearest 0.1 mm. at low magnification (7X objective lens) of a dissecting microscope, but that of the smaller dimensions, such as snout length, orbit diameter, premaxillary length, body depth, etc., were made to the nearest 0.01 mm. at high magnification (30X objective lens). At the higher magnification each division on the disc micrometer represented 0.02 mm.

Plots of body part length against standard length indicated varying degrees of nonlinear growth in premaxillary length, snout length, head length, and in body depth. Because snout and head length were found to be affected greatly by a rapid growth of the premaxillary, snout-less-premaxillary length and head-less-snout length were plotted (fig. 4) and compared against standard length.

The relation of these body parts to standard length is best described by the allometric growth equation,

$$Y = bX_{\alpha}$$

where Y is the body part, X is the standard length, α is the ratio of the instantaneous growth rates of Y and X, and b, is a constant of proportionality, sometimes referred to as the "initial growth constant" (Simpson, Roe, and Lewontin, 1960). This equation when transformed to logarithms

$$\text{Log } Y = \text{Log } b + \alpha \text{ Log } X$$

is linear.

Because not all the points for each body part could be fitted by a single curve, they were separated into several groups, and regression lines were fitted to each group separately. The original data are plotted in figure 4, and the constants for the allometric growth equations are given in table 4. The subdivision of the data was made after they had been tested for deviations from simple allometry as suggested by Richards and Kavanaugh (1945). Such subdivision of data seems justified on the basis of the tests and on the premise that in nature relative growth may deviate considerably from simple allometry, often revealing the existence

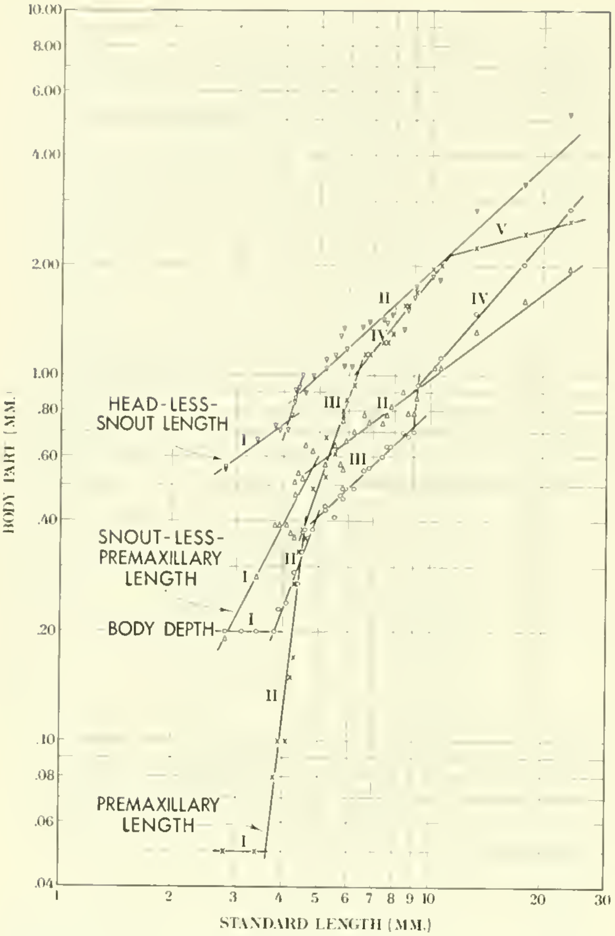

FIGURE 4.—Scatter diagram of body-part measurements plotted against standard length of larval and juvenile wahoo. Straight-line segments are regression lines fitted by the least squares method to respective groups of points. Roman numerals indicate curve segments.

of distinct growth patterns or gradients (Simpson et al., 1960). The subdivision of the wahoo data provides a satisfactory description of the growth relation.

TABLE 4.—*Constants for the allometric equation $Y=bX^a$ for larvae and juvenile wahoo collected in the central Pacific Ocean, 1950–62*

Body part	Curve segment	b	a
Premaxillary length	I	0.050	0.000
	II	$.307\times10^{-6}$	9.250
	III	$.445\times10^{-2}$	2.944
	IV	.099	1.273
	V	1.104	.276
Snout-less-premaxillary length	I	.026	1.969
	II	.167	.771
Head-less-snout length	I	.266	.727
	II	$.528\times10^{-2}$	3.500
	III	.216	.951
Depth	I	.200	.000
	II	$.428\times10^{-2}$	2.865
	III	.085	.976
	IV	.069	1.180

Certain points should be kept in mind when interpreting the curves fitted to the wahoo data. The curves are based on a small number of observations, and some curves are based on a narrow range of standard lengths. Since there is little variability in the wahoo data, the small number of observations appear adequate. The narrow range in standard lengths for some curves appears to be a phenomenon of the growth of many fishes. In addition, it is known that shrinkage of fish larvae occurs in preserved specimens. It is known also that maximum shrinkage occurs within the first few months of preservation and that shrinkage is small after 1 or 2 years, provided there is no drastic change in the amount and concentration of the preservative. As all wahoo specimens had been preserved more than 4 years and were treated in the same manner, the effects of shrinkage are thought to be negligible.

A difficulty in dealing with changes in body form in wahoo larvae is that the snout grows much more rapidly than do other parts of the body; this differential growth influences comparisons based on standard length. To determine how snout length influences standard length, I computed regressions of body parts on standard length and on standard length-less-snout length for the four body parts shown in figure 4. Both regression lines showed allometric growth in all four body parts. Since the regressions based on standard length fit the data better than do those based on standard length-less-snout length, standard length was used as the basis of comparison.

Head and Its Components

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. In larvae of this size, head length is nearly one-third of the standard length, but, in larvae 6.6 mm. long, it represents one half the standard length. This large increase in head length is due mostly to rapid growth of the premaxillary.

Five separate curves are required to describe premaxillary growth in wahoo 2.8 to 23.7 mm. long (fig. 4 and table 4). The first curve (larvae 2.8 to 3.4 mm. long) shows no increase in premaxillary length ($\alpha = 0.000$), but the second (larvae 3.8 to 4.4 mm. long) and third curves (larvae 4.5 to 6.2 mm. long) indicate positive allometry ($\alpha = 9.250$ and 2.944, respectively), i.e., the premaxillary grows at a higher rate than standard length or α is greater than 1.0. The fourth curve (larvae 6.6 to 10.7 mm. long) shows only slight positive allometry ($\alpha = 1.273$) and the fifth curve (larvae 13.2 to 23.7 mm. long) represents negative allometry ($\alpha = 0.276$), i.e., the premaxillary grows at a lower rate than standard length or α is less than 1.0.

Growth of the snout less premaxillary can be described by two curves. The first curve (larvae 2.8 to 4.5 mm. long) shows positive allometry ($\alpha = 1.969$), but the second curve (larvae 4.6 to 23.7 mm. long) shows negative allometry ($\alpha = 0.771$).

Because the very rapid growth of the snout (premaxillary included) would mask the growth of the remainder of the head and unduly influence head-length measurements, the head-less-snout length was examined. Regression lines for head-less-snout length are markedly different from those for snout-less-premaxillary and for premaxillary length (fig. 4). In larvae smaller than 4.1 mm., the head-less-snout length increases relatively slower than standard length ($\alpha = 0.727$), but, in larvae between 4.2 and 4.4 mm. long, it increases much faster ($\alpha = 3.500$). Above 4.5 mm. the growth rates of head less snout and standard length are nearly alike ($\alpha = 0.951$).

The sharp increase in the premaxillary and snout affects the appearance of the jaws considerably. In larvae shorter than 4.3 mm., the lengths of the upper and lower jaws are equal (table 5); this condition is typical of larvae of yellowfin tuna, skipjack tuna, and frigate mackerel. At a length of 4.4 mm., however, the upper jaw becomes longer than the lower and remains longer throughout the rest of the larval stages (the difference in length is still apparent in the 23.7-mm. juvenile). The greatest difference in jaw lengths is in larvae between 9.0 and 9.2 mm. long, whose ratios of upper to lower jaw are 1.25:1. This inequality diminishes progressively in larger individuals; in the 23.7-mm. juvenile, the upper jaw is only slightly longer than the lower (ratio, 1.07:1). In the adults the lower jaw is slightly longer than the upper.

TABLE 5.—*Ratios of upper jaw length to lower jaw length, upper jaw length to head length, and lower jaw length to head length by standard length for larval wahoo collected in the central Pacific Ocean, 1950–62*

Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length	Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length
Mm.				*Mm.*			
2.8	1.00	0.562	0.562	5.8	1.08	0.683	------
3.1	------	------	.545	5.8	1.12	.631	0.562
3.4	1.00	.530	.530	5.9	1.12	.681	.607
3.8	1.00	.508	.508	6.2	1.15	.707	.615
3.9	1.00	.550	.550	6.6	1.17	.697	.597
4.1	1.00	.575	.575	6.8	1.17	.712	.606
4.2	1.00	.585	.585	7.4	1.18	.676	.574
4.3	1.00	.600	.600	7.6	1.15	.712	.620
4.3	1.00	.588	.588	7.8	1.21	.728	.603
4.3	1.00	.576	.576	8.4	1.23	.755	.616
4.4	1.06	.606	.572	8.7	1.24	.731	.590
4.5	1.07	.605	.563	9.0	1.25	.718	.575
4.6	1.08	.658	.610	9.2	1.25	.714	.572
4.8	1.10	.671	.610	10.2	1.24	.745	.602
5.2	1.06	.632	.595	10.7	1.23	.769	.626
5.2	1.09	.661	.604	13.2	1.20	.692	.576
5.5	1.07	.658	.612	17.8	1.22	.692	.565
5.7	1.08	.627	.577	23.7	1.07	.578	.542

The length of each jaw relative to head length also changes significantly. In larvae smaller than 4.3 mm., the ratios of upper and lower jaws to head length are between 0.508:1 and 0.600:1 (table 5). In larvae larger than 4.4 mm., however, the length of the upper jaw increases sharply to a maximum ratio of 0.769:1 in the 10.7-mm. larva, and the lower jaw attains a maximum ratio of 0.626:1. In larvae above 10.7 mm., the ratio of jaw to head length decreases for each jaw; at a length of 23.7 mm. the ratios of the upper and lower jaws to head length are only 0.578:1 and 0.542:1, respectively.

Jaw development is also unequal in larval and juvenile *Scomberomorus* (Hildebrand and Cable, 1938; Eckles, 1949). As in larval wahoo, the longer upper jaw of *Scomberomorus* can be attributed to increased growth of the premaxillary. The premaxillary and head lengths of the wahoo were compared with the same measurements of sierra mackerel (*S. sierra*) and skipjack tuna from the eastern Pacific Ocean (Carlsberg Foundation's "Dana" Expedition 1928-30 and Inter-American Tropical Tuna Commission) and central Pacific Ocean (Bureau of Commercial Fisheries Biological Laboratory, Honolulu) (table 6).

All available data are included in table 7, although the comparison is restricted to individuals between 7.0 and 17.0 mm. because the full range of sizes for the three species was not identical. The ranges of ratios of premaxillary length to head length and the ratios of premaxillary length to standard length are distinctive for each species, and without overlap among the three. The ratio of premaxillary length to head length is largest in wahoo and smallest in skipjack. The lower and upper limits of the range for sierra mackerel (0.221:1-1.250:1) are about 1.71 and 1.54 times greater, respectively, than those for skipjack (0.129:1-0.163:1), and the lower and upper limits of the range for wahoo (0.332:1-0.413:1) are 2.57 and 2.53 times greater, respectively, than those for skipjack. Logarithmic plots of the premaxillary length against standard length (fig. 5) show this more clearly.

TABLE 6.—*Measurements of standard length, head length, and premaxillary length, and ratios of premaxillary length to standard length and premaxillary length to head length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna*

Size	Specimens	Average measurements			Premaxillary length/standard length	Premaxillary length/head length
		Standard length	Head length	Premaxillary length		
Mm.	*Number*	*Mm.*	*Mm*	*Mm.*		
Wahoo						
2.0-2.9...	2	2.8	0.8	0.05	0.018	0.062
3.0-3.9...	3	3.7	1.1	.08	.022	.073
4.0-4.9...	9	4.4	1.7	.28	.064	.165
5.0-5.9...	7	5.6	2.5	.71	.127	.284
6.0-6.9...	3	6.5	3.1	1.08	.166	.348
7.0-7.9...	3	7.6	3.5	1.26	.166	.360
8.0-8.9...	2	8.6	3.8	1.57	.183	.413
9.0-9.9...	2	9.1	4.2	1.68	.185	.400
10.0-10.9...	2	10.4	4.9	1.99	.191	.406
13.0-13.9...	1	13.2	6.4	2.25	.170	.352
17.0-17.9...	1	17.8	7.4	2.46	.138	.332
23.0-23.9...	1	23.7	9.8	2.64	.111	.270
Sierra mackerel						
7.0-7.9...	2	7.4	3.2	.75	.101	.234
11.0-11.9...	2	11.6	5.0	1.25	.108	.250
12.0-12.9...	3	12.6	5.4	1.33	.106	.248
13.0-13.9...	1	13.1	5.9	1.33	.097	.227
14.0-14.9...	1	14.0	6.4	1.58	.113	.247
15.0-15.9...	2	15.1	6.6	1.54	.102	.234
16.0-16.9...	1	16.2	6.8	1.50	.093	.221
17.0-17.9...	1	17.3	7.0	1.75	.101	.250
18.0-18.9...	2	18.7	7.2	1.62	.087	.225
Skipjack tuna						
5.0-5.9...	3	5.6	2.3	.30	.054	.130
6.0-6.9...	4	6.7	2.8	.46	.069	.164
7.0-7.9...	1	7.8	3.6	.50	.064	.139
8.0-8.9...	2	8.5	3.8	.62	.073	.163
10.0-10.9...	1	10.2	4.6	.67	.066	.146
11.0-11.9...	1	11.8	5.6	.83	.070	.148
12.0-12.9...	2	12.6	5.4	.83	.067	.154
13.0-13.9...	4	13.4	5.5	.77	.057	.140
14.0-14.9...	4	14.2	5.7	.77	.054	.135
15.0-15.9...	3	15.4	5.8	.75	.049	.129
16.0-16.9...	2	16.4	6.8	.96	.058	.141
17.0-17.9...	1	17.6	6.4	.91	.052	.142
18.0-18.9...	1	18.1	6.4	.91	.050	.142
23.0-23.9...	2	23.9	8.3	.96	.040	.116

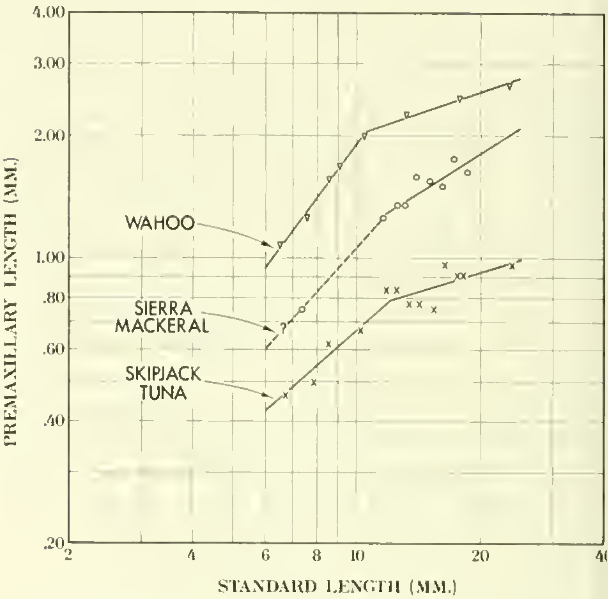

FIGURE 5.—Scatter diagram of premaxillary lengths plotted against standard length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna. Line segments are regression lines fitted by the least-squares method.

These large differences in the ratios of premaxillary length to head length suggest that the size of the premaxillary may be of generic significance. This view is contrary to Conrad's (1938) opinion that the long, pointed premaxillary, thought to be so characteristic of the genus *Acanthocybium*, "is an unfortunate illusion." Conrad based his opinion upon the closeness of the ratios of premaxillary length to skull length of *Scomber* and *Acanthocybium*, 0.23:1 and 0.24:1, respectively; however, a careful check of his ratio for *Scomber* indicates a possible error.

Conrad defined premaxillary length as "the length of premaxillae anterior to the dermethmoid" and length of skull as the length "from anterior tip of premaxillae to posterior tip of supra-occipital crest." He did not give the species name or the source of his *Scomber* measurements, but judging from his numerous citations of Allis (1903) concerning this genus, it is very likely that the measurements were obtained from the figure of *S. scomber* by Allis. Using the reference points defined by Conrad,

TABLE 7.—*Meristic counts of larvae and juvenile wahoo* [1]

Standard length	Myomeres			Branchiostegal rays	Teeth [2]				Fin spines and rays					Caudal fin rays	
	Pre-anal	Post-anal	Total		Upper jaw	Lower jaw	Palatine	Vomerine	First dorsal	Second dorsal plus finlets	Anal plus finlets	Pectoral	Pelvic	Dorsal (principal and secondary)	Ventral (principal and secondary)
Mm.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
2.8	26	39	65	0	0	0	0	0	0	0	0	0	0	0	0
2.8	29	35	64	0	0	0	0	0	0	0	0	0	0	0	0
3.1	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.4	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.8	30	35	65	0	0	0	0	0	0	0	0	0	0	0	0
3.9	27	37	64	0	0	0	0	0	0	0	0	0	0	0	0
4.1	27	37	64	0	1	0	0	0	0	0	0	0	0	0	0
4.2	29	35	64	0	2	1	0	0	0	0	0	0	0	0	0
4.3	29	36	65	0	3	4	0	0	0	0	0	0	0	0	0
4.3	29	35	64	0	D	D	0	0	0	0	0	0	0	0	0
4.3	30	35	65	0	8	9	0	0	0	0	0	0	0	0	0
4.4	29	35	64	0	7	7	0	0	0	0	0	0	0	0	0
4.5	27	37	64	0	7	8	0	0	0	0	0	0	0	0	0
4.6	27	38	65	0	9	7	1	0	0	0	0	0	0	0	0
4.8	27	37	64	0	10	10	2	0	0	0	0	0	0	0	0
5.2	27	37	64	0	13	13	2	0	0	0	0	0	0	0	0
5.2	27	38	65	1	16	14	2	0	0	0	0	0	0	0	0
5.5	26	38	64	2	15	12	2	0	0	0	0	0	0	0	0
5.7	27	38	65	4	14	14	2	0	0	0	0	0	0	0	0
5.8	28	36	64	3	16	14	2	0	0	0	0	0	0	3+0	3+0
5.8	30	35	65	5	17	15	2	0	0	0	0	0	0	3+0	2+0
5.9	27	36	63	4	17	16	2	0	0	0	0	0	0	3+0	2+0
6.2	26	39	65	5	17	15	3	0	0	0	0	0	0	4+0	3+0
6.6	32	32	64	6	18	16	3	0	0	3	4	4	0	5+0	4+0
6.6 (est.)	27	36	63	5	D	D	D	D	0	5	4	5	0	5+0	4+0
6.8	31	34	65	6	23	20	1	0	2	7	7	4	Bud	7+0	4+0
7.4	26	38	64	6	20	17	3	0	3	9	8	5	Bud	7+0	5+0
7.6	27	37	64	7	21	18	3	0	4	11	10	6	0	7+0	6+0
7.8	29	35	64	6	20	18	3	1?	5	12	11	6	0	6+0	5+0
7.9 (est.)	26	38	64	6	20	20	3	0	5	12	11	7	0	7+0	5+0
8.4	28	37	65	7	22	21	3	1	6	15	14	10	Bud	9+2	8+0
8.7	26	37	64	7	24	20	3	1	6	16	16	11	Bud	9+4	8+2
9.0	26	39	65	7	23	21	3	1	8	20	18	11	Bud	9+3	8+1
9.2	30	35	65	7	24	20	4	1	8	20	19	11	Bud	9+4	8+3
10.2	27	37	64	7	23	20	5	1	10	21	20	12	I, 2	9+4	8+3
10.7	28	36	64	7	23	21	6	2	13	21	20	11	I, 4	9+4	8+3
13.2	29	36	65	7	30	25	9	2	27	23	22	14	I, 5	9+7	8+6
17.8	26	38	64	7	28	24	8	2	27	23	22	19	I, 5	9+9	8+9
23.7	--------	--------	--------	7	28	25	7	2	27	24	22	23	I, 5	9+15	8+15

[1] Standard length (mm.) and numbers of precaudal vertebrae and caudal vertebrae for each of three specimens in which vertebrae were counted were as follows: 13.2 mm.—33, 31; 17.8 mm.—32, 31; 23.7 mm.—32, 31.

[2] D = damaged.

I obtained a premaxillary length to skull length ratio of 0.11:1 for the *S. scomber* illustrated by Allis (1903), and ratios of 0.12:1, 0.12:1, 0.11:1, and 0.10:1 for four *S. japonicus* that were 220, 271, 284, and 386 mm. fork length, respectively. These ratios vary considerably from the 0.23:1 which Conrad reported for *Scomber*.

Strasburg (1964) has mentioned the presence of a small, cartilaginous pad at the tip of the lower jaw in juvenile wahoo. The pad is barely noticeable in the 4.2-mm. larva but is clearly developed in the 4.3-mm. larva. The pad assumes its characteristic conical shape in larvae more than 5.8 mm. long.

Body Depth

In many fish larvae, body depth at the pectoral fin is greatly influenced by the amount of food in the digestive tract. Furthermore, the distention of the gill cover and the bending of the body at the junction of the head and trunk also distort the body depth of fish larvae at the pectoral fin. The variability produced by this distortion can be eliminated by discarding all distorted specimens, but this measure was not possible because few wahoo larvae were available. Consequently, body depth of wahoo larvae was measured at the posterior edge of the anus, where distortions caused by bending are minimal.

Body depth follows a different course of growth from that of premaxillary length. Differences between the two growth curves are seen mainly in larger larvae (fig. 4 and table 4); where the premaxillary grows at a uniform rate in larvae 6.6 to 10.7 mm. long, the body depth increases abruptly when the larvae are about 9 mm. long, and where the premaxillary grows relatively slower than standard length in larvae larger than 10 mm. ($\alpha = 0.276$), the depth increases slightly faster ($\alpha = 1.180$) than the body.

Distance from Snout to Anus

Snout-to-anus distance shows positive allometry, but this phenomenon results from the sharp increase in snout length relative to standard length. If the snout length is subtracted from both snout-to-anus distance and standard length, a linear relation, $Y = -0.09 + 0.623X$, is evident (fig. 6). Thus the snout-to-anus distance, less snout length, increases 0.623 mm. for each 1.0-mm. increase in standard length, less snout length. A linear relation between snout-to-anus distance and standard length also exists in the Pacific mackerel, *Pneumatophorus diego* (Kramer, 1960).

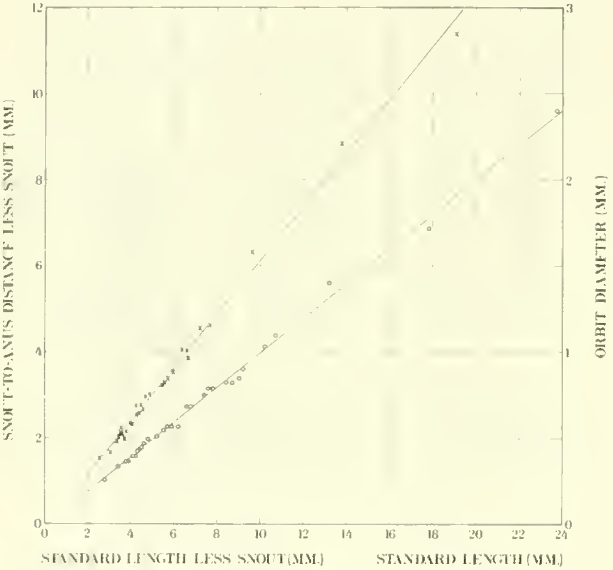

FIGURE 6.—Regressions of snout-to-anus distance less snout on standard length less snout (upper line), and orbit diameter on standard length (lower line). Lines fitted by the method of least squares.

The low rate of increase in the snout-to-anus distance of wahoo larvae is probably related to the shape of the digestive tract and the position of the anus. The digestive tract in wahoo larvae, unlike that in larvae of yellowfin tuna and skipjack tuna, is elongate, and the anus is situated near the origin of the anal fin, i.e., between the 26th and 29th myomeres, in larvae as small as 2.8 mm. (table 7). The anus maintains this relative position throughout the larval and juvenile stages. In yellowfin tuna and skipjack tuna less than 7.0 mm. long, however, the digestive tract is compact and the anus is located at a point midway between the posterior edge of the head and the origin of the anal fin, i.e., between the 9th and 11th myomeres; furthermore, the anus shifts posteriorly as the larvae increase in size, until it is situated near the origin of the anal fin in larvae 11.0 to 13.0 mm. long.

In one respect the digestive tract resembles that of larvae of yellowfin tuna and skipjack tuna: it forms a complete loop, which is clearly visible in larvae 2.8 to 5.8 mm. long (fig. 2A-D). The loop is difficult to see in larvae larger than 6.8 mm. because of the heavier abdominal musculature and the increased pigmentation over the digestive tract (fig. 3A-D). The 4.0-mm. and 5.0-mm. Pacific mackerel larvae illustrated by Kramer (1960) have a similar loop in the digestive tract.

Orbit Diameter

Throughout the size range examined, the relation of orbit diameter to standard length is linear, $Y = 0.019 + 0.0101X$, the orbit increasing 0.101 mm. in diameter for 1.0-mm. increase in standard length (fig. 6). The eye is cleft ventrally.

OSSIFICATION OF SKELETON

Myomeres, vertebrae, teeth, branchiostegal rays, fin rays, and spines were counted (table 7), and the ossification of bones was studied after the larvae had been stained with alizarin. A bone is considered as ossified if it absorbs the stain. Ossification proceeds more slowly in wahoo than it does in some other scombrids. The sequence of ossification is summarized in table 8.

Pectoral Girdle

The cleithrum is one of the first bones to ossify. The process begins in larvae about 2.8 mm. or smaller and is complete at 3.1 mm. or larger.

Upper and Lower Jaws

In the upper jaw, the development of the maxillary and premaxillary is similar to that described for *Trachurus* (Berry, 1964). The

Table 8.—*Sequence of ossification of bones of wahoo larvae*

Body part	Fish length at start	Fish length at finish
	Mm.	*Mm.*
Cleithrum	2.8	3.1
Parasphenoid	2.8	3.1
Maxillary	3.1	3.1
Dentary	3.1	3.8
Gill arch	3.4	6.8
Premaxillary	3.8	4.5
Teeth—upper jaw	4.1	-----------
Preopercular spines	4.1	-----------
Teeth—lower jaw	4.2	-----------
Preopercle	4.3	-----------
Articular	4.3	4.5
Palatine	4.3	8.4
Vomer	4.5	8.4
Palatine teeth	4.6	13.2
Branchiostegal rays	5.2	8.4
Parietal	5.7	10.7
Frontal	5.7	17.8
Caudal fin (principal rays)	5.8	8.4
Pectoral fin	6.6	23.7
Second dorsal fin and finlets	6.6	10.2
Anal fin and finlets	6.6	13.2
Vertebrae	6.8	17.8
First dorsal fin	6.8	13.2
Vomerine teeth	8.4	-----------
Caudal fin (secondary rays)	8.4	<23.7
Pelvic fin	10.2	13.2
Opercle	<13.2	-----------
Supraoccipital crest	13.2	>23.7

maxillary ossifies first in larvae about 3.1 mm. long. The premaxillary begins to ossify at about 3.8 mm., but the development is restricted to the anterior half of the jaw. Ossification proceeds posteriad until the full length is developed in larvae about 4.5 mm. long. The premaxillary essentially excludes the maxillary from the gape (i.e., from the functional biting surface of the jaw) by its position ventral to the maxillary.

The lower jaw also has two bones, the dentary and articular. The dentary first develops in larvae about 3.1 mm. long and is completely ossified in larvae over 3.8 mm. Ossification of the articular begins in larvae about 4.2 mm. long and is complete at about 4.5 mm.

Gill Arches

The gill arches do not absorb stain until the larvae are about 3.4 mm. long. After the first arch has ossified, however, subsequent arches develop in quick succession and all are completely ossified in larvae about 6.8 mm. long. As in the adults, the larvae and juveniles have no gill rakers.

Teeth

The teeth in both jaws develop at a smaller size in wahoo larvae than in yellowfin tuna larvae, but slightly later than in skipjack tuna larvae. Teeth in the upper jaw are formed only on the premaxillary, when the larvae are about 4.1 mm. long. The first few teeth appear almost simultaneously as small protuberances. In the lower jaw, teeth develop on the dentary when the larvae are about 4.2 mm. long. About seven widely spaced teeth of uniform size are present in each jaw when the larvae are about 4.4 mm. long. In larvae above 5.8 mm., smaller teeth are added near the bases of the larger ones; at 13.2 mm., one or two small teeth are usually present between two adjacent long teeth (fig. 3D). Initially, when the jaws are of equal length, the number of teeth in each is about equal. As the upper jaw protrudes beyond the tip of the lower jaw, three to four additional teeth appear on the protruded section of the upper jaw (figs. 2D and 3A-D). The three or four anteriormost teeth in the upper jaw become slightly recurved; the teeth posterior to these appear straight and more nearly vertical to the longitudinal axis of the jaw. When the juveniles attain a length of 13.2 mm., about half the number of teeth found in the adults are already ossified; however, the conical shape of the teeth of the larvae differs from the compressed and triangular teeth of the adults.

The palatine bone begins to ossify in larvae about 4.3 mm. long, and ossification is complete at about 8.4 mm. The first palatine tooth develops when the larvae are about 4.6 mm. long. The number of teeth increases slowly and reaches a maximum of nine in the 13.2-mm. larva.

The vomer begins to ossify later than the palatine, when the larvae are about 4.5 mm. long, but completes ossification at the same time as the palatine. The first vomerine tooth is developed in larvae about 8.4 mm. long; two are present at about 10.7 mm., and this number remains constant through the 23.7-mm. stage.

Preopercular Spines, Preopercle, and Opercle

Unlike the preopercular spines of skipjack tuna, which appear when the larvae are about 3.7 to 3.9 mm. total length (Matsumoto, 1958), the preopercular spines of the wahoo appear when the larvae are longer than 4.1 mm., SL. At this stage only a single spine is ossified at the angle of the preopercle. Additional spines develop slowly; at 4.3 mm., only two spines are ossified (fig. 2C). The third spine is first seen on the 4.7-mm. larva, and the fourth and fifth spines appear in larvae longer than 6.8 mm. The number of spines remains constant until the larvae attain a length of 13.2 mm., when two spines are added on the horizontal edge. The 23.7-mm. juvenile possesses the greatest number of spines: five on the horizontal and three on the vertical edge of the preopercle. The preopercular spines of the wahoo are relatively shorter than those in larvae of yellowfin or skipjack tuna, and the preopercle has already overgrown most of the spines in the 13.2-mm. juvenile.

As in larvae of yellowfin and skipjack tuna, but to a lesser degree, additional spine development occurs on a ridge on the preopercular surface anterior to the base of the preopercular spines. In larvae between 4.5 and 5.8 mm., a single short spine is present on this ridge, and two spines are developed in larvae between 6.8 and 10.7 mm. In yellowfin tuna, skipjack tuna, and black skipjack (*Euthynnus* spp.), three or more spines are already present in larvae less than 5.5 mm. total length (cf. Matsumoto, 1958, 1959).

The preopercular surface begins to ossify when the larvae are about 4.3 mm., soon after the first preopercular spine has developed. Ossification starts at the base of the preopercular spine and, as more spines are added, increases correspondingly. When the larvae are 7.4 mm. long, a small portion of the dorsal and ventral terminals of the preopercle also becomes ossified. The surface of the preopercle is almost completely ossified in the 23.7-mm. juvenile.

In larvae of yellowfin tuna, skipjack tuna, and black skipjack, between 5.0 and 6.0 mm. total length, a conspicuous spine develops in the posttemporal region of the head. This spine is absent in wahoo; instead it is represented by a bony ridge which is present throughout the larval and juvenile stages. This ridge is first apparent in the 8.4-mm. larva. A second ridge is seen dorsal to the first, and a groove appears between the two ridges in the 23.7-mm. juvenile. I presume that with continued growth of the juvenile, these two ridges unite to form a canal that becomes part of the lateral line system.

The opercle begins to ossify when the larvae are about 13.2 mm. long. Ossification progresses slowly, and the opercle is still not completely developed at 23.7 mm.

Branchiostegal Rays

The first branchiostegal ray is seen in the 5.2-mm. larva. The number of rays increases to four in the 5.7-mm. larva and to six in larvae 6.6 to 6.8 mm. long. The full complement of seven rays is generally ossified in larvae about 8.4 mm. (fig. 3B), although a 7.6-mm. larva already had seven rays. The posteriormost ray ossifies first, and subsequent ossification proceeds anteriorly.

Other Head Bones

The parasphenoid first begins to ossify in larvae 2.8 mm. or smaller, and its entire length is ossified in about 3.1 mm.

It is difficult to determine the initial development of the frontal and parietal bones because these bones did not stain sufficiently in some of the specimens. The first sign of ossification appears in the 5.7-mm. larva. The parietal bone develops faster than the frontal bone and is completely ossified in larvae 10.7 mm. long. The frontal bone, on the other hand, is completely ossified only in the 17.8-mm. larva and the 23.7-mm. juvenile.

In contrast to these three bones, ossification of the supraoccipital crest, which develops only after nearly all the fin rays and vertebrae have completely ossified, starts in larvae about 13.2 mm. long. Ossification is completed only after the individuals exceed 23.7 mm.

Fins

The sequence of fin formation in wahoo larvae is similar to that of jack mackerel and Pacific mackerel (Ahlstrom and Ball, 1954; Kramer, 1960); the only difference is in the length of body at which fin development commences. In all fins, the actinotrichia first develop in the larval fin fold. These are replaced by definitive rays, lepidotrichia, which are branched, jointed rays composed of bone. Fin spines arise by alteration and fusion of the joints of the lepidotrichia. The fins will be discussed in the order of their formation: (1)

larval pectoral (without rays), (2) caudal, (3) pectoral, (4) second dorsal and anal, (5) first dorsal, and (6) pelvic.

Larval pectoral fins.—The larval pectoral fins are formed on the smallest larva, 2.8 mm. long. The fin membrane is large and fanshaped, and fin rays do not develop until the larvae are well past 6 mm. (table 8).

Caudal fin.—The caudal fin of wahoo develops first as a thickening ventral to the posterior portion of the notochord in larvae about 4.4 mm. long (fig. 2C). As the size of this thickening increases, the posterior portion of the notochord turns upward; at this stage the larvae are shorter than 6.8 mm. (fig. 3A). This thickening eventually develops into the hypural bones.

The principal caudal rays, those that are ultimately supported by the hypural bones, develop before any of the secondary caudal rays are formed. When the larvae are about 5.8 mm. long, the first two to four rays near the middle of the posterior edge of the hypural thickening develop almost simultaneously. The midline separating the ultimate dorsal and ventral lobes of the tail is clearly discernible, owing to the wide spacing between the two medial rays. The initial group of rays lies at an oblique angle to the notochord, but as the posterior part of the notochord turns upward, it pulls the rays up to a horizontal position. Subsequent ray development proceeds dorsally and ventrally from the medial rays. As in most percomorph fishes, there are 17 principal caudal rays in the wahoo: 9 are dorsal and 8 ventral to the midline of the fin. All the principal rays are completely developed in larvae over 8.4 mm. long (fig. 3B).

The secondary caudal rays first appear on larvae about 8.4 mm. long with the development of two dorsal rays anterior to the tip of the notochord. The sequence of ossification is from posterior to anterior for both the dorsal and ventral secondary rays. At a length of 23.7 mm., the caudal fin has 15 dorsal and 15 ventral secondary rays, which is within the range for adults.

The shape of the caudal fin changes as the rays are being developed. At first the larval caudal fin, represented by the median fin fold, is roundly lobed. As the principal rays develop, the initial medial rays are longer than the rest of the fin fold. With the flexion of the notochord and the subsequent shift in position of the rays to a horizontal plane, the fin outline becomes angular (fig. 3A). After all the principal rays have developed, the dorsal and ventral rays begin to outgrow the medial rays, so that the posterior margin of the fin gradually assumes a square and finally a forked shape. The fork in the caudal fin is evident in the 10.7-mm. larva (fig. 3C) and is pronounced in larvae above 13.2 mm. long (fig. 3D).

Pectoral fins.—The larval pectorals already are present in the smallest wahoo (fig. 2A). The initial pectoral rays begin to develop near the dorsal part of the fin when the larvae are about 6.6 mm. long, and are much shorter than the pectoral membrane. At a length of 8.4 mm., these rays extend to the margin of the larval pectoral fin. As is usual in pectoral-fin development, the dorsal rays appear first. Twenty-three pectoral rays are developed in the 23.7-mm. juvenile. This total is within the range for adults.

Second dorsal fin and finlets.—The base of the second dorsal fin first appears as a thickening on larvae as small as 5.8 mm., and the first rays are developed in larvae 6.6 mm. long. The first two or three rays develop simultaneously near the middle of the fin; subsequent rays develop anteriorly and posteriorly to these. The first few finlets develop before the formation of the anteriormost ray of the second dorsal fin. The last finlet, however, develops only after the formation of all the second dorsal fin rays.

In the early stages of development, it is extremely difficult to differentiate rays from finlets. Consequently, the number of ray and finlet elements for the larvae were combined. A similar grouping for the adults shows that the full complement of rays and finlets for the second dorsal fin ranges from 20 to 22 (table 2). As discussed earlier, two elements, which are separated in the larvae, form the last adult finlet. Consequently, the total number of larval fin ray and finlet elements comparable with those of the adult must be more than 21. The full complement of rays and finlets in the second dorsal is already present in the 13.2-mm.

larva (table 7). The last two finlets in the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are situated very close together but are not yet fused.

Anal fin and finlets.—Ossification of anal fin rays occurs simultaneously with that of the second dorsal fin. Although subsequent development of rays and finlets is nearly identical with that of the second dorsal fin and finlets, the adult complement is not attained until the juvenile has exceeded 10.7 mm. long. All the rays and finlets are completely formed in the 13.2-mm. larva. As in the dorsal finlets, the last two anal finlets on the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are very close together, their bases nearly touching each other.

First dorsal fin.—As in the anal and second dorsal fins, the base of the first dorsal fin thickens when the larvae are about 6.2 mm. long. The first two or three spines develop almost simultaneously and are first seen in the 6.8-mm. larva (fig. 3A). The first spines are short (0.10 mm.), and, unlike the sequence of ray development in the anal and second dorsal fins, subsequent spines are added only posteriorly. Additional spines develop slowly; the number increases from 2 in the 6.8-mm. larva to 10 in the 10.2-mm. larva. In larvae over 10.2 mm. long, however, the spines are added more rapidly, so that 27 spines are already evident in the 13.2-mm. larva (table 7).

The height and shape of the fin also change with growth of the larvae. Larvae between 8.4 and 8.7 mm. long have all six spines of equal height. Shortly thereafter, the anteriormost spine becomes the longest and each succeeding spine is shorter than the one preceding it. A concavity in the fin outline becomes noticeable after the eighth or ninth spine has ossified (i.e., when the larvae are about 9.0 or 10.0 mm. long). All spines after the ninth are about equal in height (fig. 3D).

Pelvic fins.—The pelvic fins are the last to develop. They appear first, as a protuberance on the ventral contour of the body below the pectoral fin base, in larvae between 6.8 and 9.0 mm. Unlike the interradial membranes of other fins, which develop from the larval fin fold, those of the pelvic fins grow out from the fin base. Initially, the spine and one or two rays ossify almost simultaneously and are first noticed in the 9.2-mm. larva. Both spine and rays are short (0.29 mm.), but their length increases rapidly, so that in the 17.8-mm. larva (table 3), the longest pelvic fin ray (1.44 mm.) is almost as long as the longest pectoral ray (1.50 mm.). The full complement of one spine and five rays is completely formed in juveniles longer than 13.2 mm.

Vertebral Column

In the wahoo, as in many other fishes, the vertebral spines ossify before the centra. A vertebra is considered to be developing as soon as any part begins to ossify, as indicated by stain absorption. Because the anterior abdominal vertebrae, which develop first, lack haemal spines, the ossification of the neural spines is the first stage of vertebral development. Neural spines first appear in wahoo at 6.7 mm. The number of neural spines increases rapidly from 1 in the 6.8-mm. larva to 10 in the 8.4-mm. larva. All the neural and haemal spines are partially or completely ossified in the 13.2-mm. larva, and all the centra in the 17.8-mm. juvenile.

The sequence of development of the centra is from anterior to posterior, in the order of their position. As in the Pacific mackerel, ossification of the centrum starts at the dorsal and ventral portions and progresses laterally until the two ossified portions meet at the midline. The dorsal portion of the first six centra and the ventral portion of the first four are ossified in the 8.4-mm. larva. In the 13.2-mm. larva, the first 10 centra are completely ossified, the 11th to 22d centra are partially ossified, and the dorsal and ventral portions of the 23d to 34th centra are beginning to ossify. The ventral portions of the two centra anterior to the last one, which give rise to the urostyle, also begin to ossify in the 13.2-mm. larva. The remaining 26 centra become ossified between lengths of 13.2 and 23.7 mm.

The urostyle first develops in larvae about 8 mm. long and is completely ossified in larvae larger than 13 mm. In the 13.2-mm. larva, only about half the area of the largest hypural element is ossified. The early development of the urostyle and the last two centra is similar to the ossification in Pacific mackerel (Kramer, 1960). All the bones in the hypural complex are completely ossified in the 17.8-mm. larva.

The neural spines are initially based on the anterior end of their centra. As each centrum grows progressively longer, the base of the corresponding neural spine seems to shift posteriorward, until it is near the middle of the centrum. This change in position of the base of the neural spine is evident in the last six vertebrae (excluding the terminal vertebra) of the 23.7-mm. juvenile. In the adult the bases of the 50th to 59th neural spines have shifted further caudad, to the posterior edge of their corresponding centrum.

The haemal spines, which first appear near the anterior part of the centra, generally remain in their original position throughout the larval stage. In the juvenile stage the bases of the last six or seven haemal spines have shifted posteriorward to the middle of the centrum. This condition is evident in the 23.7-mm. juvenile and is similar to that found in the adult, in which the bases of the 53d to 58th haemal spines have shifted further caudad to the posterior edge of their corresponding centra. This posterior shifting of the neural and haemal spines and the simultaneous decrease in the angle formed by the spines and longitudinal axis of the vertebral column produce the narrow caudal peduncle so characteristic of the scombrids.

Unlike the Pacific mackerel, which develops zygapophyses at about 8.7-mm. body length (Kramer, 1960), the wahoo develops zygapophyses when the larvae are 17.8 to 23.7 mm. long. No zygapophysis is ossified in the 17.8-mm. larva, but in the 23.7-mm. juvenile, the neural prezygapophyses of the 2d to 61st vertebrae and the neural postzygapophyses of the 1st to the 60th vertebrae are ossified. Some differences exist between juvenile and adult neural postzygapophyses of vertebrae near the caudal end. Neural postzygapophyses are widely separated from the bases of the neural spines in juveniles, but in adults those of the 54th to 62d vertebrae have become partially or entirely fused to the neural spines, as each succeeding spine gradually inclines toward the horizontal axis of the vertebral column.

The haemal zygapophyses also ossify when the larvae are between 17.8 and 23.7 mm. long. No haemal zygapophysis is developed in the 17.8-mm. larva, but most of the adult complement are ossified in the 23.7-mm. juvenile. In the latter specimen, the first haemal prezygapophysis is seen on the 27th vertebra; the first two or three appear as small projections near the anterior edge of the centrum and anterior to the base of the haemal arch. All succeeding vertebrae possess haemal prezygapophyses. These structures are presumed to develop anteriorly from the 27th vertebra as the juveniles increase in length, since in the adults the anteriormost haemal prezygapophysis is on the 19th to 21st vertebra.

The haemal postzygapophyses follow a sequence of ossification slightly different from that of the prezygapophyses. In the 23.7-mm. juvenile, haemal postzygapophyses are ossified on the 11th to the 60th vertebra. In the adults, haemal postzygapophyses are present on about the 6th to 57th or 58th vertebra. Consequently, I presume that, as the fish matures, ossification of haemal postzygapophyses continues anteriorly, and the postzygapophyses of the last five or six caudal vertebrae fuse with the haemal spines.

Clothier (1950) called the processes of the haemal arches the haemapophyses and named as parapophyses "the bony projections on each side of the anterior ends of the centra in the abdominal region to which the ribs are attached." I shall use these two terms as defined by Clothier. Perhaps some of the parapophyses and haemapophyses are already ossified in the 10.7-mm. larva, but this cannot be determined because the vertebral column of this specimen did not stain adequately. The anteriormost parapophysis on the side of the centrum is developed on the 13th vertebra in the 13.2-mm. larva, and the anteriormost haemapophysis is developed on the 18th. In the 17.8-mm. larva and the 23.7-mm. juvenile, the anteriormost parapophysis is seen clearly on the third vertebra in the dorsal third of the centrum, which is the adult condition. The parapophyses on succeeding vertebrae are situated progressively lower on the side of the centrum, and the first pair of haemapophyses at the ventral surface of the centrum is ossified on the 17th vertebra.

To trace the development of the haemapophyses on larger wahoo, two juveniles, 152- and 159-mm. SL taken from stomachs, and two adults, 1,066- and 1,252-mm. fork length, were examined. Additional information from an adult 1,468 mm. long (type of length measurement not clearly defined) was obtained from Conrad (1938). The vertebra on which the anteriormost haemapophysis is located, listed in the order of fish size (length in millimeters shown in parentheses), is as follows: 17th (23.7), 12th (152), 13th (159), 14th (1,066), 15th (1,252), and 16th (1,468). This sequence suggests first, that after the initial ossification of the anteriormost haemapophysis on the 17th vertebra in the smallest juvenile, other haemapophyses develop anteriorly until the maximum number has been attained at a length of about 152 mm.; second, that as the fish increase in size, the position of the anteriormost haemapophysis apparently moves posteriorly, probably because of a gradual upward shift in the position of the haemapophysis on the centra as the vertebrae increase in size.

The development of the anteriormost haemal arch also suggests a shift in position. The position of the initial haemal arch shifts from the 23d or 24th vertebra in the juveniles to the 26th or 27th vertebra in the adults.

OCCURRENCE AND DISTRIBUTION OF WAHOO

The adult wahoo are generally found in tropical and subtropical waters and are taken as incidental catches by surface trolling and longlining. In both types of fishing, however, the catches are small: in the central Pacific Ocean only 236 wahoo were caught in 8,937 line-hours of trolling (Murphy and Ikehara, 1955) and 58 wahoo were taken on 14 POFI (now BCF Biological Laboratory, Honolulu) longline fishing cruises, during which 94,128 hooks had been fished at 450 fishing stations (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955). Results of surface trolling within a few kilometers of land in the Line Islands in 1955 have led Iversen and Yoshida (1957) to infer that wahoo prefer shallow depths and are more abundant close to shore.

To determine whether the wahoo are taken on the longline more commonly in inshore than in offshore areas (areas less than or greater than 110 km. from land), I plotted the locations where wahoo were taken on the longline (fig. 7) and tested the catch data. The catches in the two areas were not statistically significant.

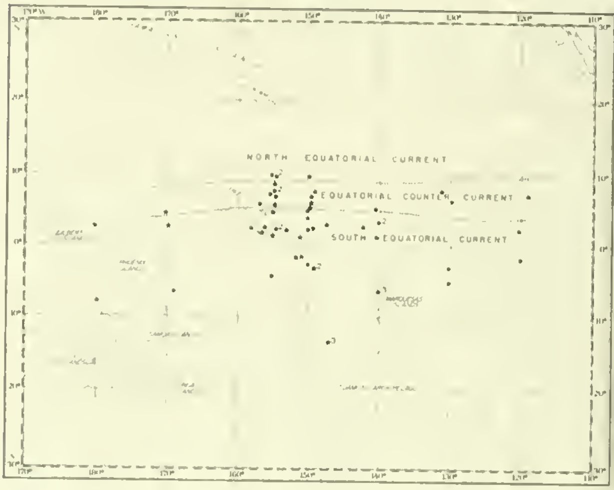

FIGURE 7.—Location and number of adult wahoo taken during 14 POFI (now Biological Laboratory, Honolulu) longline cruises. Each star represents a single wahoo taken at a fishing station. A star and number show catches of two or more wahoo per station. Broken lines around islands indicate a distance of 110 km. from land. Major currents in the central Pacific Ocean are shown.

Larval wahoo were found also in tropical and subtropical waters of the Pacific Ocean between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. Interestingly, differences between the catches of wahoo larvae in inshore and offshore areas (areas less than or greater than 110 km. from land) were not significant; 12 larvae were caught in 11 of 566 plankton net hauls in inshore areas and 26 larvae were caught in 23 of 1,077 net hauls in offshore areas. The distribution of catches of larvae (fig. 1), moreover, resembled that of the adults taken on the longline.

Of particular interest to this study are (1) the captures of larvae and adults far from land and (2) the scarcity of larvae in the Equatorial Countercurrent (fig. 1), although adults have been taken there on a number of longline stations (fig. 7). One site of larval capture, lat. 8°42′ S. and long. 115°39′ W., was 2,057 km. from the nearest land mass, Ducie Island. This distance is only 181 km. less than the greatest distance from land where an adult wahoo has been taken. Six other capture sites were farther than 900 km. from land. Although adults frequent the Equatorial Countercurrent, they may not spawn there in appreciable numbers. Only one wahoo larva was taken there, representing a catch rate of 0.14 larva per tow.

More adult wahoo are taken around the Hawaiian Islands in summer (April through August) than in other seasons (Welsh, 1949). Seasonal trends are absent, however, near the Equator and around the Line Islands (Iversen and Yoshida, 1957), as they also were in the longline catches made on the 14 POFI cruises (table 9) between lat. 14° N. and 14° S. Most of the fishing on these cruises was done between lat. 9° N. and 8° S.

TABLE 9.—*Adult wahoo caught on 14 POFI longline cruises in the central Pacific Ocean between lat. 14° N. and 14° S.*

Month	Wahoo caught	Catch of wahoo/ 1,000 hooks
	Number	*Number*
January	1	0.29
February	8	.96
March	6	1.33
April	0	.00
May	2	.29
June	4	.72
July	6	2.70
August	14	.69
September	6	.40
October	3	.30
November	4	.37
December	4	.56

TABLE 10.—*Catch rate of wahoo larvae and number of plankton samples collected by months in three areas*[1] *of the central Pacific Ocean, 1950–62*

Month	Area I		Area II		Area III		All areas
	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Plankton samples
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
January	0.0	34	1.8	109	-------	-------	143
February	.0	23	1.0	96	3.4	29	148
March	.0	83	2.1	195	4.2	48	326
April	.0	32	6.1	49	-------	-------	81
May	4.2	96	2.9	34	-------	-------	130
June	4.8	21	1.8	111	-------	-------	132
July	6.1	66	2.4	42	-------	-------	108
August	3.3	180	1.2	81	-------	-------	261
September	3.2	31	0.0	45	-------	-------	76
October	2.6	39	1.3	75	-------	-------	114
November	0.0	53	0.0	46	0.0	2	101
December	-------	-------	8.7	23	-------	-------	23
All months	2.6	658	2.0	906	3.8	79	1,643

[1] Area I from lat. 30° to 15° N.; Area II from lat. 14° N. to 14° S.; Area III from lat. 15° to 25° S.

Monthly catches of larval wahoo show similar trends (table 10). In the area near the Hawaiian Islands (Area I) larvae were taken only in the summer and early fall (May through September), but in the equatorial region (Area II) they were taken in nearly all months of the year.

SUMMARY

Thirty-eight wahoo larvae were taken in a 1-m. plankton net during 32 cruises of the Bureau of Commercial Fisheries research vessels, *Hugh M. Smith* and *Charles H. Gilbert*, in the central Pacific from May 1950 to July 1962. The standard lengths of these specimens ranged from 2.8 to 17.8 mm. In addition, six adults and four juveniles from other sources were examined.

Published accounts of adult wahoo give a vertebral formula, 23 to 33 precaudal +31 to 34 caudal = 54 to 66 total vertebrae, which is an extremely wide range of variation for a fish belonging to the Scombridae. All studies based on examination of specimens indicate only minor variation (31 to 33) in the number of precaudals. Consequently, I conclude that the wide range of precaudal vertebrae first credited to Kishinouye (1923) is incorrect and that the lower figure of 23 precaudals must be a typographical error—a transposition of digits from 32 to 23.

The number of first dorsal spines is constant at 27 in both juveniles and adults. The number of finlets in juveniles is greater than that in adults by one, owing to the fusion of the last two finlets in adults.

Body pigmentation is relatively sparse in larvae smaller than 3.4 mm.; a few melanophores occur on the tip of each jaw, one in each primordial nasal cavity, one on the ventral margin of the caudal peduncle, and a series of about nine evenly spaced along the dorsal surface of the digestive tract. The most noticeable change in pigmentation occurs in larvae above 5.8 mm., when the melanophore at the caudal peduncle migrates to the base of the anal fin and there the number increases until a series of melanophores forms over the entire base of the anal fin. A similar series of melanophores develops at the base of the second dorsal fin. The only other significant increase in pigmentation is in the first dorsal fin just before the larva reaches a length of about 13.0 mm.

Premaxillary length, snout length less premaxillary length, head length less snout, body depth at anus, and snout-to-anus distance less snout show allometric growth that can be described by the equation, $Y = bX_\alpha$.

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. Most of this increase is due to the rapid growth in the premaxillary and snout. The shape and size of the mouth also are affected by the rapid growth in premaxillary and snout. Prior to attainment of 4.3 mm., both jaws have the same length; subsequently, the upper jaw protrudes beyond the lower, and at about 9.0 mm., the ratio of upper to lower jaw is 1.25:1. This ratio decreases to 1.07:1 in the 23.7-mm. juvenile, and in adults the upper jaw is equal to or slightly shorter than the lower. Before unequal jaw development begins, the ratios of upper and lower jaws to head length is between 0.508:1 and 0.601:1. After their lengths become unequal, the ratios of upper and lower jaws to head length increase to 0.769:1 and 0.626:1, respectively.

Body depth increases unevenly throughout the size range. The most rapid growth occurs in larvae between 9.0 and 9.2 mm. long.

Snout-to-anus distance less snout length is linearly related to standard length less snout length. It increases 0.623 mm. for each millimeter increase in standard length less snout length.

Unlike the digestive tract of larvae of yellowfin tuna or skipjack tuna, which is compact (anus located well ahead of the origin of the anal fin), the digestive tract of wahoo larvae is fully extended (anus located close to the origin of the anal fin). The digestive tract of wahoo resembles that of yellowfin tuna and skipjack larvae in that it forms a complete loop.

Orbit diameter is linearly related to standard length. It increases 0.101 mm. for each millimeter increase in standard length.

Ossification of bones and hard parts differs only slightly from the sequence found in jack mackerel and Pacific mackerel. The sequence in wahoo is as follows: Cleithrum and parasphenoid, maxillary and dentary, gill arches, premaxillary, teeth of upper jaw, preopercular spines, teeth of lower jaw, preopercle, articular, palatine, vomer, palatine teeth, branchiostegal rays, parietal, frontal, principal rays of caudal fin, pectoral fin, second dorsal and anal fins simultaneously, vertebrae, first dorsal fin, vomerine teeth, secondary caudal rays, pelvic fins, opercle, and supraoccipital crest.

Wahoo larvae were found in tropical and subtropical waters between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. The numbers of larvae and adults caught inshore (less than 110 km. from land) and offshore were not significantly different. Wahoo larvae were taken mostly during the summer in the area north of lat. 15° N., and throughout the year along the Equator between lat. 14° N., and 15° S.

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Shoji Ueyanagi, of the Nankai Regional Fisheries Research Laboratory, Japan, sent me a photostatic copy of Kishinouye's work (1908); and Elbert H. Ahlstrom, Robert H. Gibbs, Jr., Bruce B. Collette, and Frederick H. Berry critically reviewed the manuscript.

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SEASONAL DISTRIBUTION AND RELATIVE ABUNDANCE OF PLANKTONIC-STAGE SHRIMP (*Penaeus spp.*) IN THE NORTHWESTERN GULF OF MEXICO, 1961[1]

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ABSTRACT

Planktonic stages of shrimp (*Penaeus* spp.) were sampled systematically in the Gulf of Mexico near Galveston, Tex., during January-December 1961. The Gulf-V plankton net was used every 3 weeks at stations established at water depths of 14, 27, 46, and 82 m. The study area encompassed about 20,725 km.^{2}

Trends in seasonal abundance of larvae varied with depth. At 14-m. stations a unimodal trend was observed, and peak abundance was during May to September. In deeper waters a bimodal trend was apparent; peak abundance extended from late summer through fall. At all depths, trends in larval abundance increased as bottom water temperatures increased.

Postlarvae were taken in plankton tows during January to April but were most abundant during August to December.

Distinct shifts in the areal distribution of larvae and postlarvae were apparent. During January to March, larvae were restricted to water deeper than 14 m. and shallower than 82 m. whereas postlarvae occurred in all depths. This situation was generally reversed in April to August, when larvae were at all depths, but the distribution of postlarvae was restricted. In September to December, distribution patterns of larvae and postlarvae were generally similar.

On the basis of this study and laboratory experiments on larval development and postlarval growth rates as affected by temperature, support is given to the premise that brown shrimp larvae or postlarvae, or both, overwinter in waters over the Continental Shelf.

The shrimp fishery in the Gulf of Mexico has expanded rapidly within the past 20 years and is now the most valuable fishery in the United States. Since 1950 the yearly harvest has fluctuated around 200 million pounds. Although about six members of the family Penaeidae are taken in the fishery, only three species—the brown shrimp, *Penaeus aztecus* Ives; the pink shrimp, *P. duorarum* Burkenroad; and the white shrimp, *P. setiferus* (Linnaeus)—contribute significantly to the catch.

Before 1959, research designed to provide management programs for optimum utilization of these shrimp stocks did not increase at the same rate as the value of this fishery. In 1959, however, the Bureau of Commercial Fisheries began a program of shrimp research that has expanded considerably during the past 7 years. The general aims of the program were stated by Kutkuhn (1963). The present study of the seasonal distribution and abundance of planktonic-stage *Penaeus* spp. in the northwestern Gulf of Mexico is a part of this research.

Considerable information has been published on the early life history of the white shrimp (Weymouth, Lindner, and Anderson, 1933; Burkenroad, 1934; Pearson, 1939; Anderson, King, and Lindner, 1949). Brown and pink shrimp have similar early life histories, although bathymetric and geographic distributions of the adults are different. In general, these shrimp spawn in waters over the Continental Shelf; brown shrimp spawn at least as far as 198 km. (110 nautical miles) offshore in depths as great as 110 m. The eggs are slightly denser than sea water and settle to the bottom when spawned. After hatching, the young become planktonic and develop through three larval (naupliar, protozoeal, and mysis) and several postlarval stages. They enter the estuaries as postlarvae, grow rapidly to subadult size, and then migrate offshore to complete their growth and spawn.

The earlier work on white shrimp provides

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little information about the seasonal distribution, abundance, and taxonomy of planktonic stages of penaeids in the Gulf of Mexico. Until recently the most extensive work available was that of Pearson (1939), who not only described planktonic stages of several penaeids from specimens obtained from plankton hauls, but also provided information on seasonal occurrence and distribution of postlarval white shrimp. More recently, descriptions of plank-

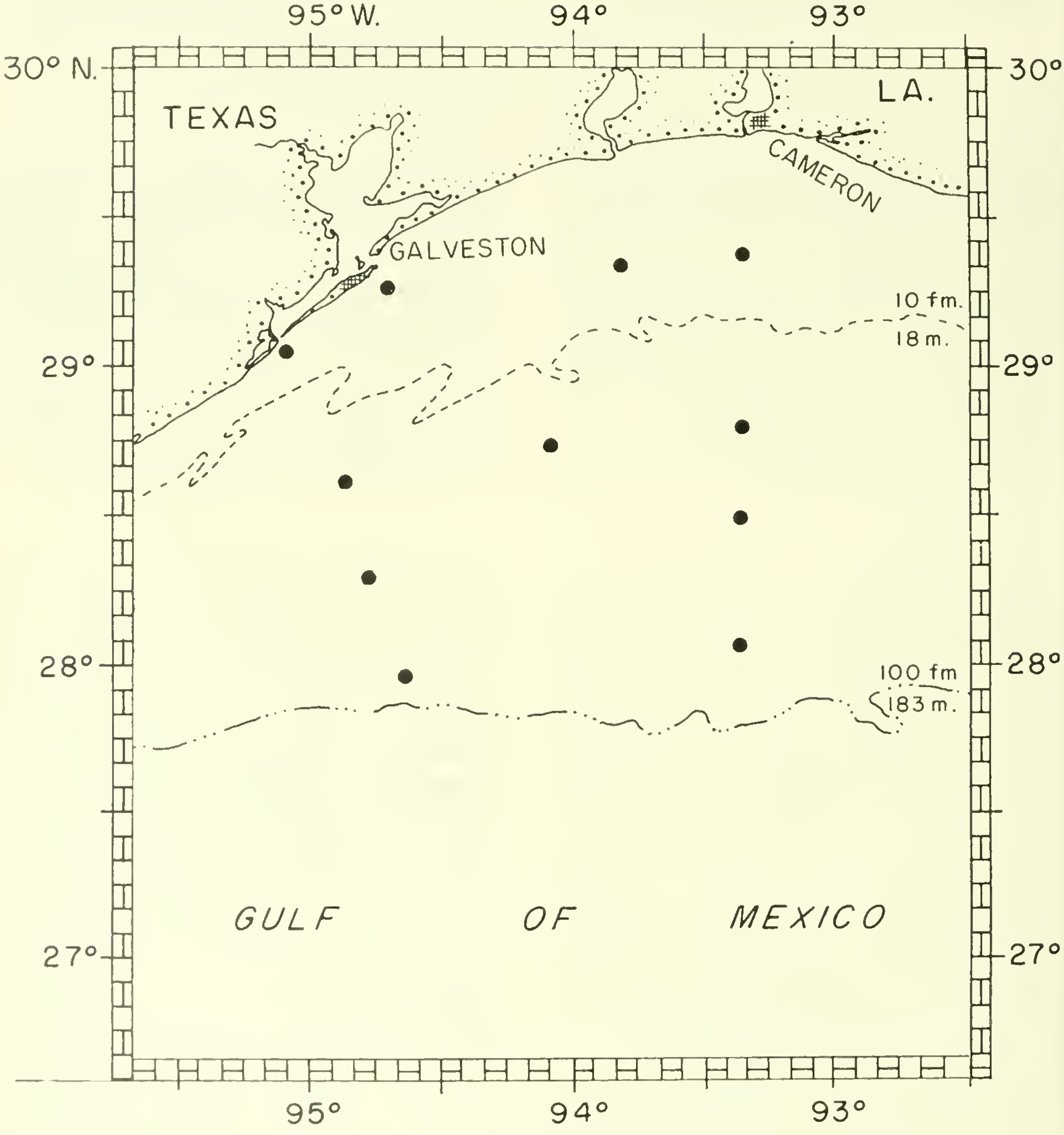
95° W.
94°
93°
30° N.
30°
TEXAS
LA.
CAMERON
GALVESTON
10 fm.
18 m.
29°
29°
28°
28°
100 fm
183 m.
GULF OF MEXICO
27°
27°
95°
94°
93°

FIGURE 1.—Location of sampling stations for shrimp larvae in 1961.

tonic stages have been published for the pink shrimp by Dobkin (1961); for the seabob, *Xiphopeneus kroyeri* (Heller) by Renfro and Cook (1963); and for the rock shrimp, *Sicyonia brevirostris* Stimpson by Cook and Murphy (1965). All three species occur in the northern Gulf.

Because of the limited amount of taxonomic material available, as well as the occurrence of about 35 penaeids (Burkenroad, 1936; Springer and Bullis, 1956; Bullis and Thompson, 1965) in the Gulf of Mexico, one of the major problems in this study was the identification of the planktonic stages. Although H. L. Cook (personal communication) has been able to rear the planktonic stages of brown, white, and pink shrimp, differentiation of the species among these forms is not yet possible. Consequently, penaeids encountered in plankton samples were identified only to genus by using the generic key developed by Cook (1966a). Data on only *Penaeus* spp. are presented in this report.

METHODS AND MATERIALS

STUDY AREA

During 1961, sampling was conducted at 11 stations (fig. 1) over an area of about 20,725 km.^{2} (8,000 square miles). During cruises at 3-week intervals, plankton hauls were made at stations where water depth was about 14, 27, 46, and 82 m.

SAMPLING GEAR AND CALIBRATION

Plankton samples were obtained with the Gulf-V plankton net described by Arnold (1959). This gear consists of a metal frame, to which a conical monel net with a mesh size of 31.5 strands per centimeter is attached. The diameter of the net mouth is about 40.5 cm. Plankton was collected in a cup attached to the end of the net. After each tow the net was thoroughly washed down and the plankton removed and preserved in 5 percent Formalin.[2]

Estimates of water volume filtered during each tow were calculated from a flowmeter positioned in the center of the net mouth. Both TSK and Atlas flowmeters, calibrated by the technique outlined by Ahlstrom (1948), were used. Each tow lasted 20 minutes, and towing speeds averaged 4.6 km. per hour (2.5 knots). Flowmeter readings indicated that during each tow the net filtered about 100 m.^{3} of water. Catches are reported in numbers of organisms per 100 m.^{3} of water strained.

DEPTHS FISHED AND TOWING CABLE PROFILE

Each of four depths was fished for 5 minutes during each tow: 3 m. above the bottom, two intermediate depths, and 3 m. below the surface. The two intermediate depths fished were equally spaced vertically within the water column and depended on the total water depth. Sampling depths were determined by the trigonometric function of the wire angle and length of towing cable. Realizing that this technique assumed the profile of the towing cable to be a straight line, we attached a bathykymograph[3] (Model T-1a, Marine Advisors, Inc.) to a Gulf-V net and made tests to determine the reliability of this technique. Results are given in table 1.

A plot of mean actual depths vs. calculated depths provides an estimate of the error between the actual and assumed towing cable profiles (fig. 2). Agreement was close to a

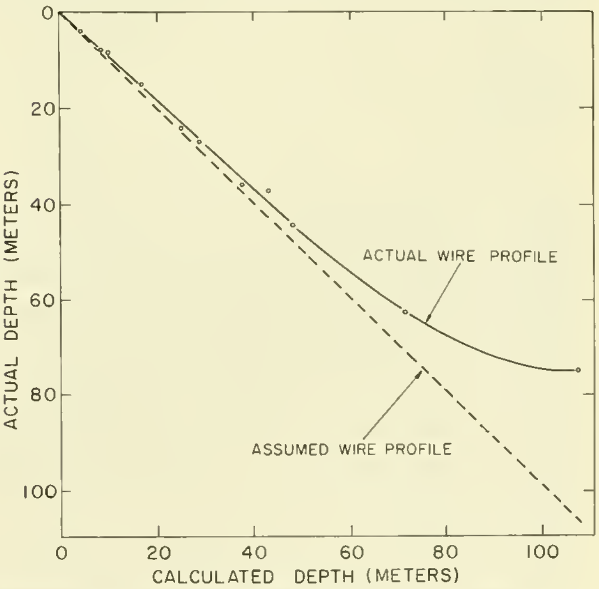

FIGURE 2.—The calculated and actual profiles of the towing cable attached to a Gulf-V plankton net.

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

[3] Calibration accuracy ± 1 percent full scale. Sensitivity 0.5 percent of full scale.

TABLE 1.—*Results of tests to determine reliability of calculated sampling depths attained by using wire angle and length of towing cable*

Observations	Calculated depth	Average actual depth	Range of observed depths
Number	*Meters*	*Meters*	*Meters*
5	3	3	2–4
1	5	4	–
1	8	7	–
7	10	8	4–10
16	17	17	8–22
16	25	24	17–35
10	29	27	24–32
3	38	36	25–48
10	43	37	32–45
10	48	44	35–57
13	71	63	55–77
3	107	75	64–88

depth of 50 m., but became progressively poorer beyond this depth. Consequently, the deepest samples from stations in 82 m. of water probably were taken at a distance above the bottom that averaged considerably greater than the intended 3 m.

DAY VS. NIGHT CATCHES OF PLANKTONIC-STAGE *PENAEUS SPP.*

The oblique-step tow was used throughout this study in an attempt to eliminate possible differences in day and night catches caused by diurnal migrations of larval shrimp. Russell (1925, 1928) has shown that, in general, decapod larvae undergo diurnal vertical migrations. More recently Temple and Fischer (1965) observed similar migrations in planktonic stages of penaeid shrimp in the northwestern Gulf of Mexico when temperature profiles (bathythermograph traces) indicated a stratified water column.

Hydrographic conditions over the Continental Shelf in the northwestern Gulf of Mexico appear to be seasonal, as there are definite times when temperatures of the waters are either stratified or isothermal (Harrington, 1965). The time and extent of these seasons vary, however, depending on total water depth and to some degree on distance offshore. In general, water is stratified at a total depth of 14 and 27 m. during May to July, at 46 m. during May to September, and at 82 m. during April to October. In other months, temperatures are essentially isothermal.

Average day and night catches were calculated for stations at which water was stratified and for those at which the water column was isothermal (table 2). Hauls with no shrimp were excluded. Catches made at the 82-m. stations also were excluded because no larvae appeared to be present during either the day or night at certain times of the year, and water deeper than 50 m. was not sampled adequately. After a test of homogeneity indicated a need for logarithmic transformation of the data, statistical treatment revealed that day and night catches did not differ significantly during either stratified or isothermal conditions. As used in this study, the oblique-step tow apparently did prevent possible differences in day and night catches caused by diurnal migrations of larval shrimp.

TABLE 2. *T-test of average catches of planktonic-stage Penaeus spp. in day and night samples during different temperature conditions in the northwestern Gulf of Mexico, 1961*

[Number per 100 m.^{3} of water strained]

Stage	Water stratified			Water isothermal		
	Day	Night	"t"[1]	Day	Night	"t"[1]
Nauplius	12.5	10.0	0.468	24.1	14.5	0.948
Protozoea	67.2	42.7	.314	28.0	54.7	.515
Mysis	22.2	11.7	.673	13.8	12.3	.263
Postlarva	.0	7.3	....	15.4	12.6	.345
All stages	64.5	19.2	1.214	41.7	38.8	.092

[1] "t" value at .05 level.

ASSOCIATED PHYSICAL DATA

In addition to the plankton sampling at each station, temperature and salinity measurements were taken with a Foxboro Dynalog at selected depths. Temperatures were recorded to 0.1° C. and salinities to 0.1 p.p.t. (parts per thousand).

LABORATORY PROCEDURES

In the laboratory, plankton samples were transferred from 32-fluid-ounce (9.6 dl.) jars to 8-fluid-ounce (2.4 dl.) jars, and the 5 percent Formalin solution was replaced by a new 5 percent solution with glycerin and borax added. Each sample was examined under a microscope at magnifications that ranged from 0.7X to 6.0X. All planktonic stages of penaeids were removed, sorted to developmental stage, identified to genus, and counted. Postlarvae of the genus *Penaeus* were measured and identified to species by using characteristics described by Baxter and Renfro (1967).

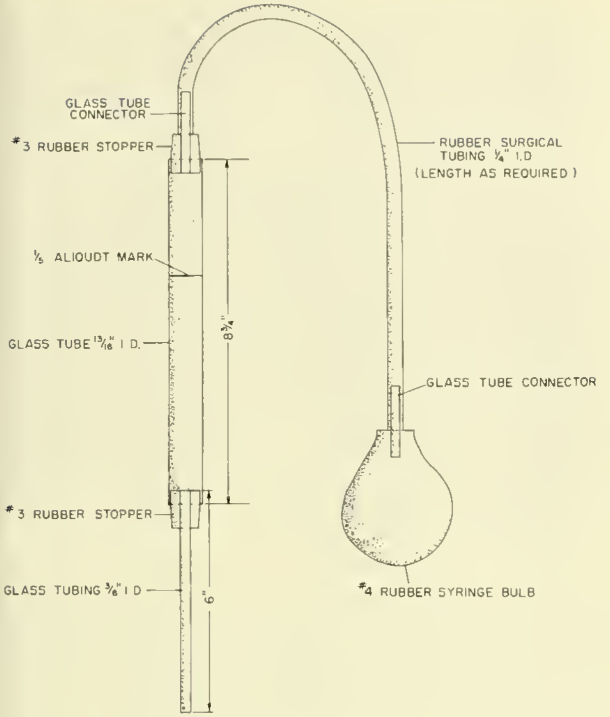
GLASS TUBE CONNECTOR
#3 RUBBER STOPPER
RUBBER SURGICAL TUBING ¼" I.D (LENGTH AS REQUIRED)
⅕ ALIQUOT MARK
GLASS TUBE 13/16" I.D.
8¾"
GLASS TUBE CONNECTOR
#3 RUBBER STOPPER
GLASS TUBING 3/16" I D
6"
#4 RUBBER SYRINGE BULB

FIGURE 3.—Syringe device used for subsampling plankton.

The amount of each sample examined depended on the settled volume of plankton. Hauls in which the settled volume was less than 25 ml. were examined in their entirety; when sample volume exceeded 25 ml., only one-fifth of the total sample was examined. Aliquots were extracted directly from the samples with a syringe device (fig. 3). Subsampling accuracy was checked by applying chi-square tests to pooled counts from aliquot sizes ranging from one-fifth to four-fifths of the total sample (table 3). These tests indicated that the subsampling technique provided adequate estimates of total counts.

TRENDS IN SEASONAL ABUNDANCE AND THEIR IMPLICATIONS

Seasonal trends in abundance for all planktonic stages of *Penaeus* spp. were determined for 14-, 27-, 46-, and 82-m. stations (table 4). Cumulative yearly totals showed that the greatest catch per unit of effort for each stage was made at the 46-m. stations.

Distinct trends in abundance for all planktonic stages combined were evident at each of the four depths (fig. 4). Two peaks of abundance were evident at each depth, but abundance was always much greater during the second peak. The time of greatest abundance was during May to August in 14 m. of water, August to November in 27 m., and September to November in 46 and 82 m. In general, peak abundance was attained at a progressively later time in the year with an increase in water depth. In addition, observed increases in abundance and increases in temperature of bottom waters at each depth were closely parallel, suggesting a possible direct relation.

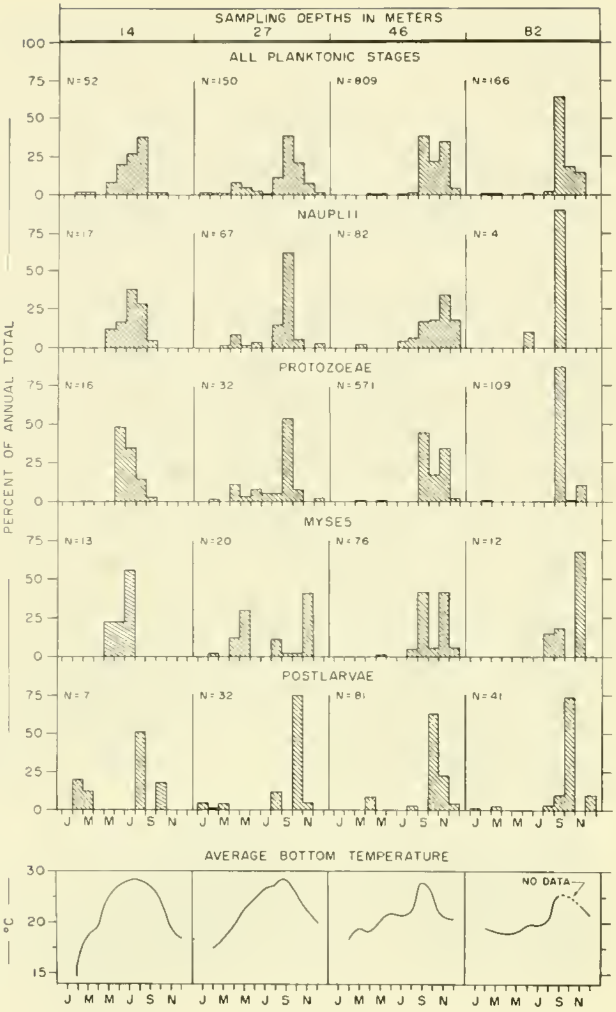

FIGURE 4.—Seasonal abundance trends of planktonic-stage *Penaeus* spp. and average bottom temperature by station depths in 1961.

At the 27-, 46-, and 82-m. stations, larval stages, excluding postlarvae, were taken in

TABLE 3.—*Results of tests to determine subsampling accuracy for obtaining total counts of larval shrimp in plankton samples*

Larvae in sample	Fraction of sample examined							
	One-fifth		Two-fifths		Three-fifths		Four-fifths	
	Samples tested	Chi-square value	Samples tested	Chi-square value	Samples tested	Chi-square value	Samples tested	Chi-square value
Number	*Number*		*Number*		*Number*		*Number*	
1-10	7	[1]6.155	5	0.630	2	0.060	2	1.841
11-49	22	.156	7	.070	3	.205	2	.033
50-99	9	.312	5	.090	4	1.370	4	.027
100-199	10	2.056	8	.873	8	.005	6	.986
200-299	3	1.488	2	3.195	2	2.111	2	[1]4.380
600-699	1	.010	1	1.145	-----	-----	-----	-----
900-999	1	.385	1	.132	1	.312	1	1.204

[1] Significant at .05 level; chi-square table value = 3.841.

plankton hauls during both periods of increased abundance. At 14-m. stations, however, larval stages were encountered only during May to September. Postlarval stages made up the entire catch in February and March. Exclusion of postlarvae from the catches, consequently, results in a unimodal trend in larval abundance at the shallowest stations and a bimodal trend at deeper stations.

The difference between depths in timing of peak larval abundance is believed caused by the bathymetric distribution of the white and brown shrimp, which constitute about 98 percent of the total commercial shrimp landings from this area. Lindner and Anderson (1956), reporting on the bathymetric distribution of white shrimp in Louisiana and Texas waters, indicated that although a few adults may be in water deeper than 27 m., the bulk of the population is in shallower water. The spawning period in May to August, indicated by the occurrence of larvae in our plankton hauls at 14- and 27-m. stations, agrees closely with the spawning season of white shrimp along the Louisiana and Texas coasts postulated by Lindner and Anderson (1956).

Periods of increased larval abundance measured at 27-, 46-, and 82-m. stations reflect, we believe, the spawning activity of brown shrimp. The bathymetric distribution of adult brown shrimp along the Texas and Louisiana coasts can be inferred from the statistics of commercial landings supplied by the U.S. Fish and Wildlife Service. These data reveal that although brown shrimp concentrations vary seasonally, the greatest number of adults usually are in water 27 to 46 m. deep during the fall. In addition, Renfro and Brusher (manuscript in preparation),[1] who determined

TABLE 4.—*Monthly catch of Penaeus spp. by depth, 1961*

[Number of shrimp per 100 m.^{3} of water filtered]

Depth and planktonic stage	Month												Cumulative total
	January	February	March	April	May	June	July	August	September	October	November	December	
14 meters.													
All stages	0.0	1.4	0.7	0.0	4.4	10.5	13.9	18.6	1.0	1.2	0.0	0.0	51.7
Nauplii	.0	.0	.0	.0	2.2	2.9	6.5	4.7	.6	.0	.0	.0	16.9
Protozoeae	.0	.0	.0	.0	.0	7.6	5.2	2.3	.4	.0	.0	.0	15.5
Myses	.0	.0	.0	.0	2.2	.0	2.2	8.1	.0	.0	.0	.0	12.5
Postlarvae	.0	1.4	.7	.0	.0	.0	.0	3.5	.0	1.2	.0	.0	6.8
27 meters:													
All stages	1.3	.9	2.1	11.6	7.8	4.5	1.9	17.9	59.2	31.0	9.8	2.2	150.2
Nauplii	.0	.0	.7	5.8	1.0	1.9	.0	10.2	41.9	4.3	.0	1.1	66.9
Protozoeae	.0	.3	.0	3.3	.9	2.6	1.9	1.8	16.9	2.7	.0	1.1	31.5
Myses	.0	.3	.0	2.5	5.9	.0	.0	2.2	.4	.5	8.2	.0	20.0
Postlarvae	1.3	.3	1.4	.0	.0	.0	.0	3.7	.0	23.5	1.6	.0	31.8
46 meters:													
All stages	.0	.0	3.3	6.3	3.6	.0	3.3	11.8	303.9	166.6	278.2	31.9	808.9
Nauplii	.0	.0	2.6	.0	.0	.0	3.3	4.7	13.7	14.5	28.2	14.6	81.6
Protozoeae	.0	.0	.7	.0	2.4	.0	.0	1.2	258.3	97.8	200.7	9.4	570.5
Myses	.0	.0	.0	.0	1.2	.0	.0	3.5	31.9	3.6	31.7	4.2	76.1
Postlarvae	.0	.0	.0	6.3	.0	.0	.0	2.4	.0	50.7	17.6	3.7	80.7
82 meters:													
All stages	.0	1.3	.9	.0	.0	.4	.0	3.1	105.1	30.9	24.4	.0	166.1
Nauplii	.0	.0	.0	.0	.0	.4	.0	.0	3.4	.0	.0	.0	3.8
Protozoeae	.0	.9	.0	.0	.0	.0	.0	.0	95.4	.5	12.2	.0	109.0
Myses	.0	.0	.0	.0	.0	.0	.0	1.7	2.1	.0	8.1	.0	11.9
Postlarvae	.0	.4	.9	.0	.0	.0	.0	1.4	4.2	30.4	4.1	.0	41.4
Cumulative total—all stages	1.3	3.6	7.0	17.9	15.8	15.4	19.1	51.4	469.2	229.7	312.4	34.1	

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[1] "Seasonal abundance, size distribution, and spawning of penaeid shrimp in the northwestern Gulf of Mexico," by William C. Renfro and Harold A. Brusher, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.

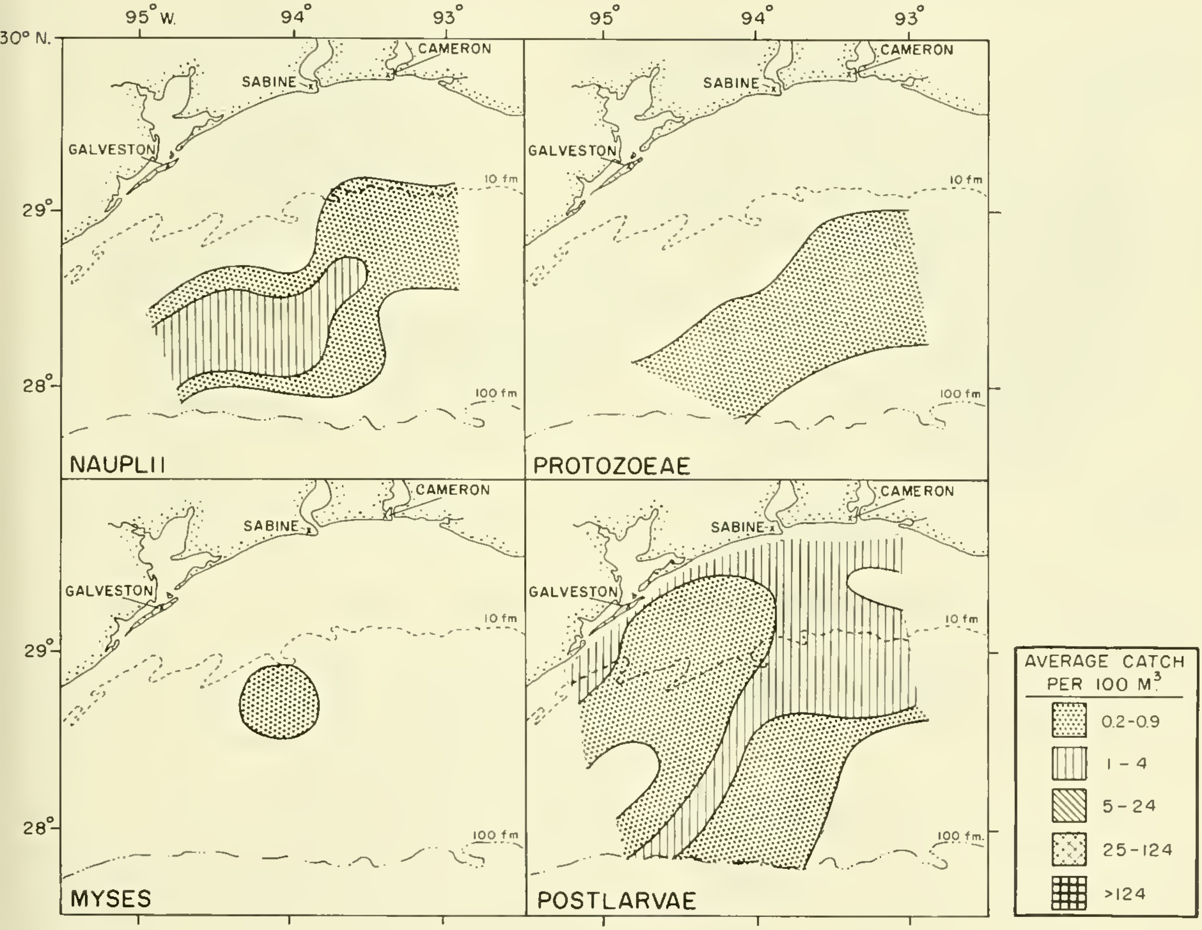
spawning seasons of the brown shrimp by ovarian examination, reported that ripe brown shrimp rarely occur in water less than 27 m. deep along the Texas and Louisiana coasts.

SPAWNING IN RELATION TO BOTTOM TEMPERATURES

Because penaeids are poikilothermic and larval abundance is apparently related directly to seasonal warming of bottom waters, we considered the possibility that spawning, indicated by the presence of naupliar stages in plankton hauls, might occur over a rather narrow temperature range. The yearly range in bottom temperatures decreased with an increase in depth. At the shallowest stations, temperatures ranged from 5.9° to 30.4° C., and at the deepest stations, from 16.8° to 26.2° C. In general, naupliar stages occurred over a temperature range of 17.0° to 28.5° C., but the magnitude of the range varied between depths (table 5). At 14-, 27-, 46-, and 82-m. stations the magnitude of the range where nauplii were taken was 3.8°, 11.5°, 8.5°, and 5.6° C., respectively.

DISTRIBUTION OF PLANKTONIC-STAGE SHRIMP

Areal distribution charts for each planktonic stage were made for January to March, April to August, and September to December. Values plotted at each station were obtained by averaging catches per 100 cm.^{3} of water filtered for


95° W.
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95°
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30° N.
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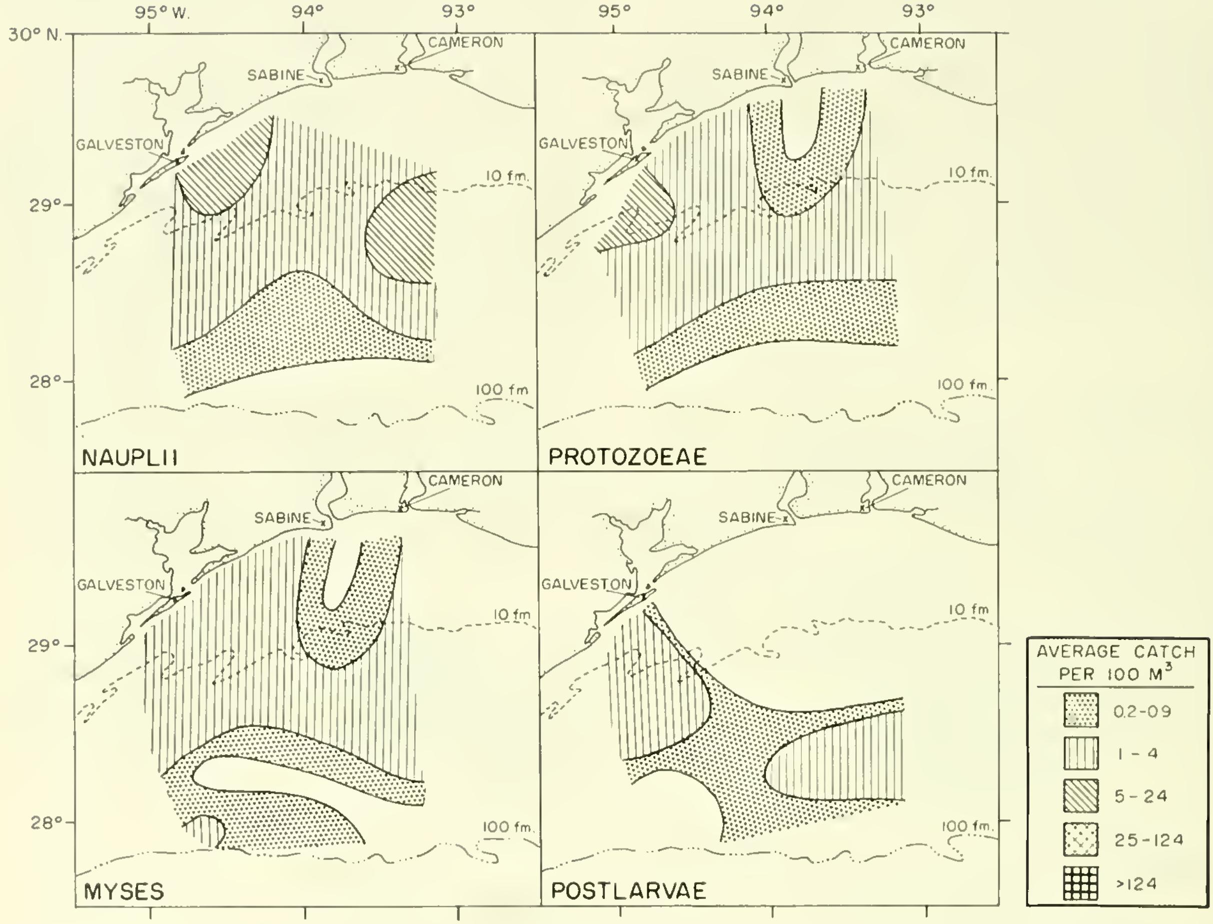
28°
29°
28°
CAMERON
SABINE
GALVESTON
10 fm
100 fm
NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M.^{3}
0.2-0.9
1 - 4
5 - 24
25 - 124
>124

FIGURE 5.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., January to March 1961.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SABINE
GALVESTON
10 fm.
100 fm
NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M³
0.2-09
1 - 4
5 - 24
25 - 124
>124

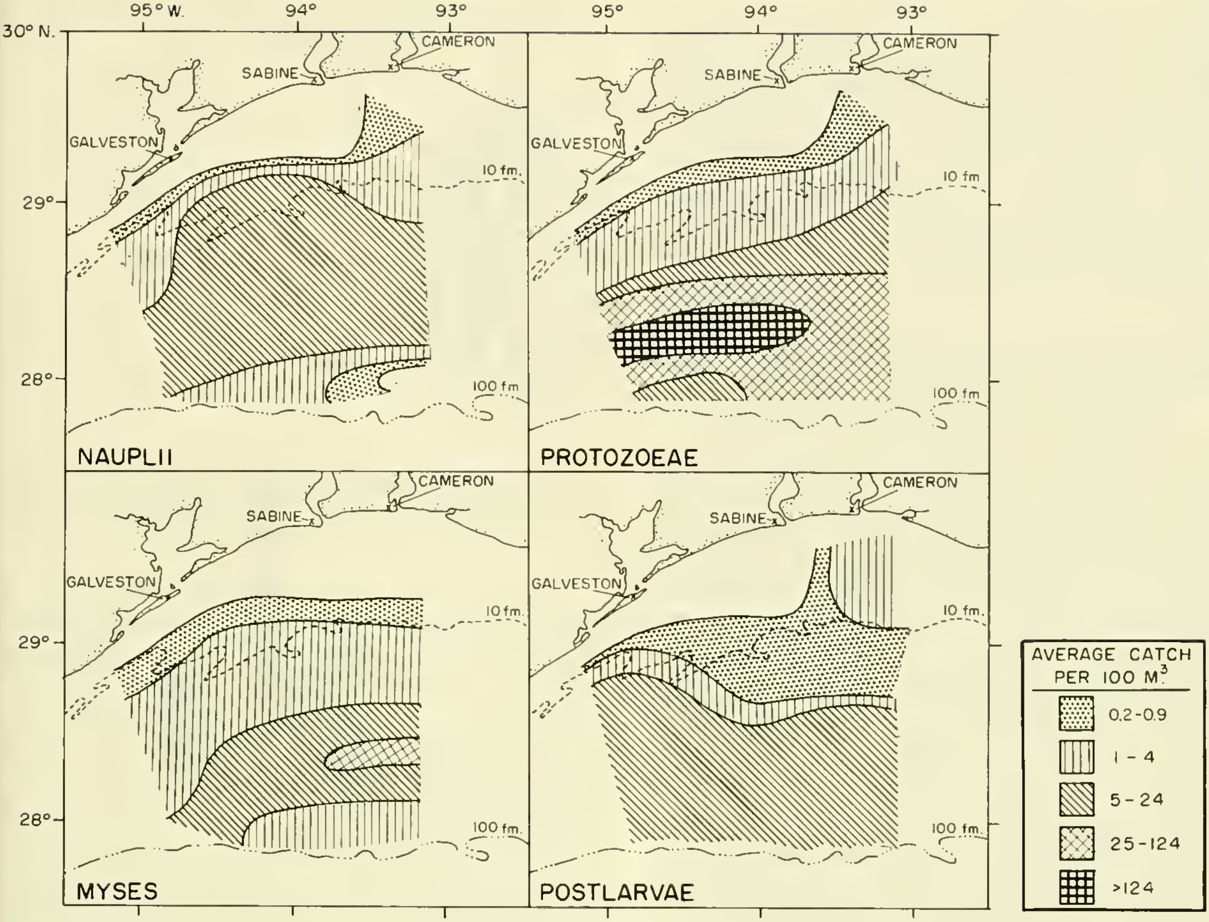
FIGURE 6.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., April to August 1961.

TABLE 5. *Yearly range in bottom temperatures and temperatures in which naupliar stages were taken in the northwestern Gulf of Mexico in 1961*

Station depth	Yearly range in temperature	Temperature in which nauplii occurred	
		Range	Magnitude of range
Meters	° *Centigrade*	° *Centigrade*	° *Centigrade*
14	5.9-30.4	24.7-28.5	3.8
27	11.9-31.0	17.0-28.5	11.5
46	14.2-27.7	19.0-27.5	8.5
82	16.8-26.2	19.9-25.5	5.6

each time period. Isopleths were then drawn to delineate areas of planktonic-stage concentrations (figs. 5, 6, and 7).

Slight shifts in the areal distribution of naupliar, protozoeal, and mysis stages were apparent. In January to March, larvae were restricted largely to waters deeper than 14 m. and shallower than 82 m.; in April to August concentrations were primarily shoreward of 46 m.; and in September to December, when the great-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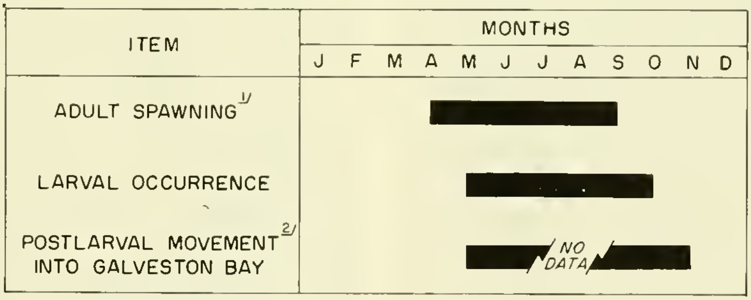
30° N.
29°
28°
29°
28°
CAMERON
SABINE
GALVESTON
10 fm.
100 fm
NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M³
0.2-0.9
1 - 4
5 - 24
25 - 124
>124

FIGURE 7.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., September to December 1961.



1/ TAKEN FROM LINDNER AND ANDERSON, 1956
2/ TAKEN FROM BAXTER AND RENFRO, 1966

FIGURE 8.—Months of spawning, larval occurrence, and postlarval movement into Galveston Bay by the white shrimp, *P. setiferus*.

est number of larvae were caught, they were restricted generally to waters deeper than 14 m. The occurrence of larvae at 14-m. stations in April to August reflects, we believe, the spawning of white shrimp in shallow waters. Similarly, increased concentrations of larvae from September to December in deeper waters indicate the spawning of brown shrimp.

The areal distribution of postlarvae during the three periods differed from that of larvae.

Postlarvae occurred throughout the area in January to March, but when abundance and areal distribution of larvae were increasing in April to August, postlarval catches were generally low and postlarvae were not as widely distributed as larvae. During the ensuing months, however, the distribution of postlarvae increased, and in September to December it closely approximated that of the larval stages.

ABUNDANCE OF LARVAE AND POSTLARVAE IN RELATION TO SPAWNING PERIODS AND POSSIBLE OVERWINTERING

Although species differentiation of the larval stages of *Penaeus* spp. is impossible at this time, we have hypothesized that trends in larval abundance observed in different depths of water are the result of differences in depth and season of spawning of white and brown shrimp. The hypothesis that greatest abundance of larvae at the shallowest stations (14 m.) follows the spawning of white shrimp is compatible with the works of Pearson (1939) and Lindner and Anderson (1956). In addition, since larval development requires 2 to 3 weeks (Pearson, 1939), agreement is also close between larval occurrence at 14-m. stations and postlarval movement of white shrimp into Galveston Bay reported by Baxter and Renfro (1967). Spawning, maximum larval abundance, and postlarval movement of white shrimp into the nursery areas are apparently completed over a 7- to 8-month period within a calendar year (fig. 8).

The chronology of spawning, larval abundance, and postlarval movement of brown shrimp into Galveston Bay is not as apparent as for white shrimp. Increasing abundance of larvae at station depths of 27 m. or deeper appears to follow closely the spawning of brown shrimp reported by Renfro and Brusher. (See footnote 4.) When compared with movement into Galveston Bay reported by Baxter (1963), however, a definite anomaly is apparent (fig. 9). Most postlarvae moved into the Bay in the spring, but the largest catches of larvae in the Gulf were made in the fall. Because similar trends in larval abundance (Fischer, 1966) and postlarval movements (Baxter and Renfro, 1967) have been observed in recent years, the possibility that techniques of sampling bias the results appears to be negligible.

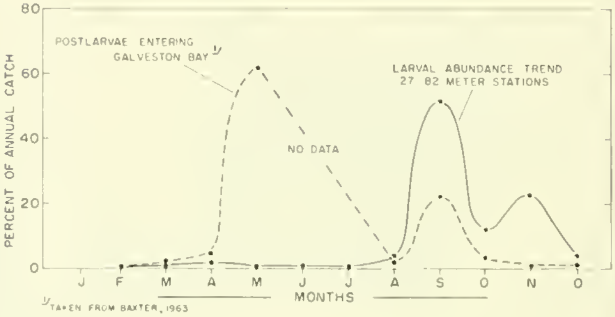


FIGURE 9.—Larval abundance trends in 27 to 82 m. of water adjacent to Galveston and postlarval movement of brown shrimp into Galveston Bay, 1961.

The difference in timing between offshore larval and inshore postlarval peaks can possibly be explained by examining seasonal abundance trends and length-frequency distributions of postlarval brown shrimp taken in plankton hauls. Postlarvae were generally taken in plankton hauls from January through April, and August through December (fig. 4). As with larvae, most postlarvae were taken in the fall. Length-frequency distributions, based on total lengths from the tip of the rostrum to the tip of the telson, reveal two distinctly different size groups (fig. 10). In January to April, most postlarvae averaged 11 to 12 mm., whereas in August to December they averaged only 6 to 7 mm.

The size difference between the two groups of postlarvae has significance when compared with length-frequency distribution of postlarvae migrating into Galveston Bay (Baxter and Renfro, 1967). Postlarval shrimp taken during the peak inshore movement average about 12 to 13 mm. in total length, and were probably represented offshore by the group of postlarvae averaging 11 to 12 mm. taken between January and April. The question still remains, however: From what spawning and peak of larval abundance did the postlarvae originate? Kutkuhn (1966) stated that the postlarvae probably originated from ". . . heightened spawning activity in offshore brown shrimp populations during February and

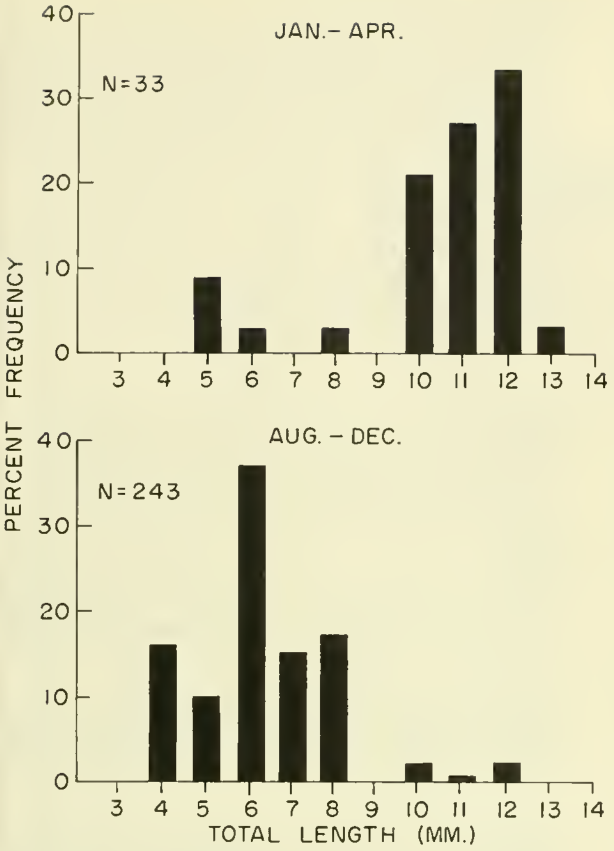


FIGURE 10.—Length-frequency distributions of postlarval brown shrimp (*P. aztecus*) taken in plankton hauls, 1961.

March. . ." Renfro and Brusher (see footnote 4), however, reported that, although brown shrimp may spawn continually throughout the year, major periods of spawning activity are in April to June and September to November. Furthermore, in the absence of large catches of larval stages during January to March 1961, the possibility arises that this spring group of postlarvae originated from a large spawning in the fall of 1960. If this is true, young brown shrimp must remain offshore either as larvae or postlarvae for a longer period than was previously suspected.

If young brown shrimp do overwinter offshore, the developmental rate of these larvae or the growth rate of the postlarvae, or both, must be slower than has been previously reported for white shrimp. Cook (1966 b), while rearing larval brown shrimp, observed retarded developmental rates at temperatures lower than 30° C. Zein-Eldin and Aldrich (1965) reported that postlarvae held in the laboratory under controlled temperature had a maximum growth rate of about 1.4 mm. per day at 32° C. and 1.1 mm. per day at 25° C. They also found that growth of postlarvae held over a 30-day period at 11° C. was practically nil, but that survival was high.

Additional support for the hypothesis that brown shrimp may overwinter before entering the nursery areas was provided by Aldrich, Wood, and Baxter.[5] They found that in the laboratory postlarval brown shrimp would burrow in response to experimentally reduced temperatures. This response usually occurred between 12° to 17° C. It appears then that under certain temperatures postlarval brown shrimp may burrow and grow at a slow rate.

Results of laboratory experiments on larval development rates, postlarval growth, and postlarval burrowing characteristics are of particular significance because temperatures similar to those tested occur in the waters over the Continental Shelf of the northwestern Gulf of Mexico (Harrington, 1965). Of even greater significance is the fact that these temperatures occur between the fall peak of larval abundance (apparently associated with brown shrimp spawning) and the peak occurrence of postlarval brown shrimp in Galveston Entrance. Additional field and laboratory work is required, however, to substantiate the hypothesis of overwintering brown shrimp larvae or postlarvae, or both, in offshore waters.

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[5] "A behavioral comparison of postlarval *Penaeus aztecus* and *P. setiferus*, with regard to burrowing as a response to reduced temperatures," by David V. Aldrich, Carl E. Wood, and Kenneth N. Baxter, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., 3 figs.

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PRINCIPAL DISEASES OF COMMERCIALLY IMPORTANT MARINE BIVALVE MOLLUSCA AND CRUSTACEA

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ABSTRACT

Diseases of commercially important marine bivalve mollusks and crustaceans can cause mortalities in natural and captive populations. Oysters have suffered frequent and extensive mass mortalities. Epizootic disease has sometimes been indicated, as for example in "dermocystidium disease," caused by a fungus, in the Gulf of Mexico, and "Delaware Bay disease," caused by a protozoan, in the Middle Atlantic States. Fungus organisms have also been implicated in "shell disease" of European oysters and a fatal disease of bivalve larvae in hatcheries. Several species of haplosporidan Protozoa cause serious mortalities of oysters and mussels. Larger animal parasites, such as larval trematodes and parasitic copepods, can affect reproduction, growth, and survival of bivalve mollusks.

Diseases of crustaceans are usually less well known. Effects of pathogens are most apparent in captive populations, where mortalities may result from outbreaks of microbial agents. Lobsters have two known bacterial diseases: the often very lethal "gaffkaemia" which occurs in wild populations, but severely affects impounded stocks; and "shell disease," caused by chitin-destroying bacteria, which is important in captive populations, probably by interfering with respiration of infected individuals. Mortalities of captive blue crabs have also been attributed to possible respiratory impairment caused by ciliate gill associates. Microsporidan Protozoa can be important parasites of crabs and shrimps; depending on their habitat within the host, they may destroy muscle tissue or gonads and have been postulated as causes of mortality. Among the larger parasites of crustaceans, rhizocephalan barnacles have long been known to cause degeneration of gonads in crabs of many species.

The described pathogens of commercial invertebrate species probably constitute only a small percentage of the many disease agents that affect marine populations. Many mass mortalities have been described in the literature; disease has been implicated in some of them, but the etiologic agent rarely has been determined precisely, and the relative importance of other environmental factors has been assessed infrequently. Diseases and parasites can also exert significant "background" effects such as continued low-level mortality, depressed reproductive capacity, and increased susceptibility to predation.

Disease control measures are possible and have been applied to a few populations of sedentary inshore marine invertebrates. Possible methods of control include quarantine, selective breeding of disease-resistant strains of shellfish, environmental manipulation (dredging of growing areas, chemical treatments, control of density of planting, and scheduled harvest), and more extensive use of artificial environments such as hatcheries and artificial ponds.

As understanding of factors that influence the numbers of animals in the sea has expanded, it has become evident that disease, among other environmental variables, can drastically affect abundance. This fact has been clearly demonstrated in populations of sedentary inshore invertebrates. Many marine invertebrate species, harvested in great numbers, constitute marine crops of high value. Some, such as mussels, oysters, clams, crabs, lobsters, and shrimps, occur in inshore or estuarine waters, and have been cultivated in varying degrees in different parts of the world. Under natural conditions or under cultivation, mass mortalities occasionally occur; here disease can be an important contributing factor.

The word "disease," as used in this paper, includes abnormalities resulting from microbial pathogens or parasite invasion, and tumors. Not included are genetically or environmentally induced abnormalities, or physiological disturbances not related to an infectious agent or parasite. For each host group considered in this review a sequence of diseases, beginning

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with those caused by bacteria (virus diseases, with but a single exception (Vago, 1966), have not been identified in marine invertebrates) and progressing to fungi, protozoans, and larger parasites, has been followed. Often a host species may be infected by several well-defined pathogens, as well as assorted parasites that have variable impact on the host population. The common and the scientific names of parasites and hosts are usually both given when the organisms are first mentioned in the text, after that either one may be used.

No general review has been made of the literature on diseases of marine invertebrates (Steinhaus, 1965), but particular groups—especially those of commercial importance—have received some attention. Dollfus (1921a), Pelseneer (1928), Ranson (1936), and Fischer (1951) have summarized information about the parasites and diseases of mollusks—particularly oysters—and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) reported on parasites and diseases of some of the commercial shrimps. Certain general aspects of invertebrate diseases, such as immune mechanisms, have been considered (Cantacuzène, 1923, 1928; Huff, 1940; Baer, 1944; Steinhaus, 1949; Stauber, 1961), and a few research groups, such as Frederik B. Bang and his associates at The Johns Hopkins University, and Albert K. Sparks and his co-workers at the University of Washington, have been concerned with comparative pathology of invertebrates (Bang, 1956, 1961, 1962; Bang and Bang, 1962; Bang and Lemma, 1962; Levin and Bang, 1964; Rabin and Bang, 1964; Sparks and Pauley, 1964; Pauley and Sparks, 1965).

Much of our knowledge about diseases of marine invertebrates concerns species of economic importance, particularly the bivalve molluscan and crustacean shellfish. This paper is concerned only with the important diseases of these two groups. We have attempted to encompass as much literature as possible from widely separated areas. Many diseases of marine invertebrates are inadequately characterized, and it is probable that others have not even been recognized. Microbial pathogens that have been implicated in mass mortalities include bacteria, fungi, and protozoans. Several of the larger parasites have been found to be pathogenic under specific conditions. Not included here are most of the parasites and diseases of noncommercial species—those species that may be of great significance in the cycles of life in the sea, but which are not of significant direct importance as food for humans. Among the groups thus excluded are gastropods and cephalopods, barnacles, copepods, and most of the smaller crabs. Also excluded are many diseases that have been incompletely described in the scientific literature.

A summarization of knowledge in any area of research, however specialized in its scope, is subjective and in some ways frustrating to the reviewer; yet a consolidation of research results can be useful, particularly to the nonspecialist. Much published information about diseases of marine bivalve mollusks and crustaceans has accumulated, and at least a representative fraction of the available literature has been considered in this paper. Preparation of a bibliography of molluscan shellfish diseases has been a continuing project of the BCF (Bureau of Commercial Fisheries) Biological Laboratory, Oxford, Md., for 6 years; this bibliography, as well as standard bibliographic and abstracting sources, has been used in preparing the manuscript. There is little representation of the Russian literature—this may be in part a reflection of the relative lack of emphasis placed on shellfish in Russian fishery research, as well as the limited availability of translations of Russian literature. Some of the older European literature, particularly that on specific parasites of invertebrates, has not been considered in this paper but is accessible through references cited in more recent publications. Although necessarily limited in content, this review attempts to assess the state of knowledge about the role of disease in two major groups of commercial marine invertebrates.

DISEASES OF BIVALVE MOLLUSCA

Most of the commercial bivalve mollusks occur in shallow inshore waters, often intertidally, where they are accessible to quantitative evaluation and observation. Unusual mortalities are more apparent here than in offshore populations. As a result, literature on mass mortalities of species such as oysters and mussels is voluminous. Disease has sometimes been demonstrated to be the cause of deaths; in other situations, disease has been strongly suspected, or the cause has not been determined. Within the past decade knowledge about molluscan shellfish diseases has increased at a greatly accelerated pace, largely because of concern about mortalities which have occurred in widely scattered populations. Literature on oyster diseases is most abundant; that on mussel and clam diseases is less voluminous.

OYSTERS

The 20th century has been a difficult and troublesome period for oysters (family Ostreidae) in many parts of the world (Orton, 1924a; Roughley, 1926; Gross and Smyth, 1946; Logie, 1956; Mackin, 1961; Sindermann, 1966c). Decline in abundance of oysters actually started late in the 19th century, probably caused in large part by indiscriminate harvesting and destruction of beds. Extensive mortalities from unknown causes also contributed to decreased oyster production. The rate of decline on the North American east coast and in other geographic areas has recently increased because of large-scale mortalities, several of which have been caused by disease. Largely because of their worldwide economic importance, oysters are among the most thoroughly studied of marine animals—especially their diseases and parasites. Interest in oyster diseases has logically arisen from catastrophic mortalities in many parts of the world. Many unsolved problems remain but the body of literature is large, and is growing rapidly.

Among the important diseases of oysters are microbial diseases and those caused by helminths and parasitic crustaceans.

Microbial Diseases

Bacteria, fungi, and protozoans are the principal causes of microbial diseases in oysters.

Bacteria.—Reports of mass mortalities of Pacific oysters, *Crassostrea gigas* (Thunberg), have been published recently in Japan (Fujita, Matsubara, Hirokawa, and Araki, 1953, 1955; Takeuchi, Takemoto, and Matsubara, 1960; Ogasawara, Kobayashi, Okamoto, Furukawa, Hisaoka, and Nogami, 1962; Imai, Numachi, Oizumi, and Sato, 1965; Kan-no, Sasaki, Sakurai, Watanabe, and Suzuki, 1965; Mori, Imai, Toyoshima, and Usuki, 1965; Mori, Tamate, Imai, and Itikawa, 1965; Numachi, Oizumi, Sato, and Imai, 1965; Tamate, Numachi, Mori, Itikawa, and Imai, 1965). Takeuchi et al. (1960) implicated a gram-negative, motile, 1– to 3–μ bacillus, probably an *Achromobacter*, in large-scale mortalities in Pacific oyster culture areas of Hiroshima Bay since 1946. Experimental infections were achieved with cultured bacteria, but the organisms could be isolated from healthy as well as sick oysters, and from sea water. Moribund oysters had diffuse cell infiltration, massive increase in bacterial numbers, and tissue necrosis.

Numachi et al. (1965) found up to 20 percent infection with gram-positive bacteria (not further identified) in oysters during mass mortalities in Matsushima Bay, Japan, in the early 1960's. The disease was called "multiple abscesses," but the authors did not think that a causal relation existed between bacteria and mortalities. A similar disease was found in 1965 by staff members of the BCF Biological Laboratory, Oxford, Md., in seed oysters (less than 1 year old) imported to the U.S. west coast from Matsushima Bay, and in adult oysters from Willapa Bay, Wash. The disease has been labeled "focal necrosis" (fig. 1). Studies of the etiologic agent and its pathogenicity

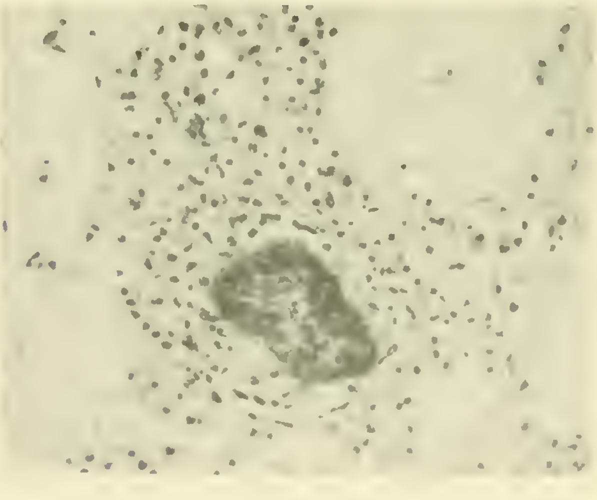

FIGURE 1.—"Focal necrosis" in connective tissue of Pacific oyster from Willapa Bay, Wash., surrounded by extensive leucocytic infiltration (× 700).

are in progress. The disease affects seed oysters as young as 6 months, as well as adults. The necrotic foci or multiple abscesses may represent the resistant or arrested disease state, and the active, fulminating phase may have already killed susceptible members of the population.

Several bacterial pathogens of bivalve larvae have been isolated (Guillard, 1959; Tubiash, Chanley, and Leifson, 1965). Identified only as *Aeromonas* sp. or *Vibrio* sp., the organisms killed larvae and juveniles of five bivalve species tested, including American oysters, *Crassostrea virginica* (Gmelin), and European oysters, *Ostrea edulis* L., but did not affect adults.

Fungi.—Oysters have several fungus diseases, some of serious consequence. Identification of fungus pathogens, especially in the early literature, has often been tentative, and only a few adequate characterizations of etiologic agents have been made.

A relatively well-known fungus infecting oysters from the Atlantic and Gulf coasts of the United States is *Dermocystidium marinum.* First described by Mackin, Owen, and Collier (1950), the pathogen has been the subject of much research. A useful diagnostic technique, based on antibiotic fortified fluid thioglycollate medium, was devised by Ray (1952, 1966b) during attempts to culture the organism. A number of authors have shown that *D. marinum* causes oyster mortalities (Mackin et al., 1950; Mackin, 1953; Andrews and Hewatt, 1954; Hewatt and Andrews, 1954; Ray, 1954a, 1954b, 1954c). Pathological changes in infected oysters were described by Mackin (1951). Invasion takes place through the gut epithelium and possibly through the mantle. The epithelium is destroyed; the parasite lyses the basement membrane and is distributed by the blood to all parts of the body (fig. 2). All tissues are invaded and damaged, and multiple abscesses are formed. Normal gonad development is inhibited, infected oysters become severely emaciated (Ray, Mackin, and Boswell, 1953; Ray, 1954b), and growth is retarded (Menzel and Hopkins, 1955b).

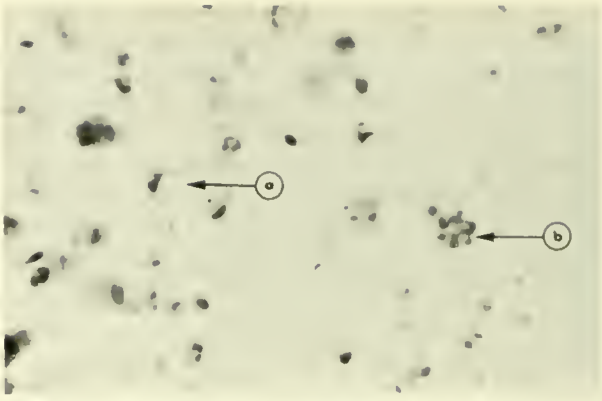

FIGURE 2.—Dermocystidium disease of American oysters. Histologic section of infected oyster showing diagnostic "hypnospore" (a) and "rosette" (b) (× 1,000).

Temperature is important in the epizootiology of dermocystidium disease (Hewatt and Andrews, 1956). Infections and associated mortalities rise during the warmer months and decline during colder periods. Mortalities decline in winter, probably because of reduced parasite metabolism, rather than elimination of the organism. Failure to find *D. marinum* consistently north of Chesapeake Bay suggests that prolonged low temperature may be a significant limiting factor. Andrews (1965) found that *D. marinum* proliferates readily only at temperatures above 25° C., and overwinters as subpatent infections. His further observation, that the partial destruction of oyster populations by a protozoan disease resulted in decreased prevalence of the fungus organism, suggests that *Dermocystidium* is dependent upon direct transmission from one oyster to another. Other evidence for direct transmission was provided by Ray and Mackin (1955).

Infections and resulting mortalities are reduced in salinities below 15 o/oo. Ray (1954b) found evidence that low salinity retarded development of terminal infections in laboratory populations. Ray and Chandler (1955) suggested that excessively high salinities may also be unfavorable for *Dermocystidium.* Mackin (1956) found a positive correlation between high salinity and high incidence of the fungus, but he observed that the salinity tolerance range was wide in experimental studies. Dilution of infective elements by inflow of fresh water was suggested as an important limiting factor and a possible control measure.

D. marinum is abundant in waters of the southern United States. Ray (1966a) who surveyed the occurrence of the fungus in the Gulf of Mexico in 1961 and 1962, found infections in 35 of 39 oyster samples, and prevalences as high as 100 percent. Hoese (1964) was able to find *D. marinum* in the digestive tracts and feces of fish, oyster drills, and crabs that had fed on dying and dead infected oysters. He speculated that transmission of the fungus might be furthered by scavengers and that scavengers may release the parasite from host tissue.

D. marinum is common in oysters from most high-salinity areas of the South Atlantic and Gulf of Mexico coasts of the United States, but is absent in a few such areas. Hoese (1963) attempted assays of water samples from different coastal locations in one section of the Texas coast to determine their inhibitory effects on development of fungus hypnospores. Although results were not conclusive, water samples from certain localities apparently stopped hypnospore development. Hoese speculated that the absence of *D. marinum* may be related to those *Spartina* salt marshes where consistently high salinities occur.

In addition to its common occurrence in *C. virginica*, *Dermocystidium* has been found in other species. Ray (1954b) reported it in the leafy oyster, *Ostrea frons* L., from Florida and in horse oysters, *O. equestris* Say, from Texas. The organism was not found, however, in the mangrove oysters, *C. rhizophorae* (Guilding), from Puerto Rico, in *O. edulis* from Holland, or in the rock oyster, *C. commercialis* (Iredale and Roughley), from Australia. *O. lurida* (Carpenter), the Olympia oyster, was experimentally infected by exposure to infected *C. virginica*. *Dermocystidium*-like organisms have also been seen in other mollusks and annelids. Andrews (1955) found what he termed "*Dermocystidium*-like" organisms in 12 of 16 mollusk species from the Chesapeake Bay area.

This important fungus pathogen of oysters continues to be the subject of much research. Knowledge of its biology has been summarized by Ray (1954b), Ray and Chandler (1955), Andrews and Hewatt (1957), and Mackin (1962). Mackin and Boswell (1956) proposed a life cycle for *D. marinum* that included a saprophytic stage leading to production of an infective spore. Recently, Perkins and Menzel (1966) described motile biflagellate stages that were also postulated to be infective to oysters. Mackin and Ray (1966) grew the organism on beef-serum agar plates and suggested that it belongs in the genus *Labyrinthomyxa*, a member of the Labyrinthulales. Culture of a *Dermocystidium* similar to *D. marinum* in chemically defined medium (Goldstein, Belsky, and Chasak, 1965) should make possible the study of isolates from many areas to determine whether one species or a species complex exists, and should permit more precise determination of the taxonomic affinities of the *Dermocystidium* group of protistan parasites.

Korringa (1947, 1951a, 1951c) reported that mortalities of the European oyster in Holland, beginning in 1930, were caused by a fungus disease characterized by formation of green or brown pustules on the inner shell surfaces. Activity of the fungus varied directly with temperature, and the outbreak was said to be intensified by widespread use of cockle shells as spat collectors. Thin parts of oyster shells were perforated by the disease agent, which proliferated after reaching the interior surfaces. The fungus had been identified earlier as a species of *Monilia* by Voisin (1931), who found the infection, called "shell disease," in 40 percent of oysters imported into France from Holland in 1931. Cole (1950) and Cole and Waugh (1956) found infections in the European oyster from Brittany and in Portuguese oysters, *C. angulata* (Lamarck), grown in England. Infections were common in beds where old shells were abundant. Cole and Hancock (1956) found the disease in almost all beds of native European oysters, and described two distinct forms: the typical one characterized by greenish rubbery warts and knobs on the inside of the shell, particularly in the region of the muscle attachment; and an atypical form in which young oysters had thickened shells with numerous white patches but had no deformation of the muscle attachment area.

Another disease of the European oyster, which may be identical to shell disease, has been misnamed "foot disease" or "maladie du pied" (Dollfus, 1921a). It has long been known on the coast of France; Giard (1894) described its etiologic agent as a bacterium, *Myotomus ostrearum*, but further definitive studies of the causative organism are needed. The disease is localized in the shell under the attachment of the adductor muscle, where it causes roughening and blistering of the shell and degeneration of adjacent muscle tissue. The muscle may become detached as irregular cysts are formed. Major mortalities occurred on oyster beds at Arcachon, France, in 1877 (Hornell, 1910; Orton, 1937). The cause was not determined, but some evidence of "foot disease" was found. Galtsoff (1964) reported the rare occurrence of the disease in the American oyster from the southern United States, but did not consider it a serious threat to oyster populations. Durve and Bal (1960) reported the rare occurrence of a shell disease which they considered to be "maladie du pied" in the backwater oyster, *C. gryphoides* (Schlotheim) from India.

Davis, Loosanoff, Weston, and Martin (1954) isolated a fungus, later described as *Sirolpidium zoophthorum* (Vishniac, 1955), from hatchery-produced oyster and clam larvae. The infections were rare, but they produced occasional epizootics that killed most of the cultured larval population in 2 to 4 days. Juvenile as well as larval bivalves were infected; growth ceased and death followed soon after infection. Infected cultures of bivalve larvae contained large numbers of motile biflagellate zoospores of the fungus. The authors speculated that an epizootic of the fungus could occur among lamellibranch larvae in nature.

There are several inconclusive reports of organisms resembling actinomycetes in oysters. Eyre (1924) reported *Cladothrix dichotoma* from oysters examined during the great mortalities of 1919–23 in western Europe. The isolate was not pathogenic in experimental studies. Dollfus (1921a) stated that Eyre's isolate was a species of *Nocardia*. Pettit (1921) also identified a *Nocardia* from *O. edulis*, but Dollfus (1921b) considered this to be merely normal cell reticulum of the oyster. Mackin (1962) described a "mycelial disease" of *Crassostrea virginica*, which he thought might be caused by an actinomycete. We have recently seen an organism similar to that described by Mackin in *C. angulata* from France.

Protozoa.—A variety of Protozoa parasitize oysters (Rosenfield, 1964; Sindermann, 1966b), and certain Sporozoa [1] are serious pathogens. Two haplosporidans, *Minchinia costalis* (Wood and Andrews) and *M. nelsoni* Haskin, Stauber, and Mackin, have caused oyster mortalities on the North American east coast within the past decade (fig. 3).

M. costalis is found in seaside bays of Maryland and Virginia, along the lower eastern shore of Virginia, and in Delaware Bay (Andrews, Wood, and Hoese, 1962; Wood and Andrews, 1962; Sprague, 1963; Haskin, Stauber, and Mackin, 1966; Couch, 1967b). First recognized in moribund and dead oysters from Hog Island Bay, Va., in 1959 by Wood and Andrews, *M. costalis* was held responsible, on the basis of epizootiological evidence, for sharp peaks of mortality in early summer. The pathogen and mortalities caused by it continue to characterize Maryland and Virginia seaside oyster populations.

The second haplosporidan species, *M. nelsoni*, has a wider distribution—from Connecticut to North Carolina. It has caused extensive mortalities and drastic decline of the oyster fishery in Delaware Bay beginning about 1957 and in lower Chesapeake Bay beginning in 1959 (Mackin, 1960; Engle and Rosenfield, 1963; Andrews, 1964). In each affected area, mortalities have often exceeded 95 percent for several years. Because of the severe impact of the *M. nelsoni* epizootic on oyster stocks of the Middle Atlantic States, a number of research groups—university, State, and Federal—have participated in scientific studies since the late 1950's, and significant papers have been published recently. Haskin et al. (1966) named the plasmodial stage of the parasite as *Minchinia nelsoni:* Couch, Farley, and Rosenfield (1966) associated the plasmodium with spore and prespore stages; and Barrow and Taylor (1966) confirmed, with immunological techniques, the association of plasmodium and spore. Andrews (1964, 1966) described aspects of the epizootiology of the disease in Virginia waters, and Haskin, Canzonier, and Myhre (1965) briefly summarized the epizootiology in Delaware Bay.

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[1] Throughout this paper an attempt has been made to conform to the revised classification of the Protozoa as proposed by Honigberg, Balamuth, Bovee, Corliss, Gojdics, Hall, Kudo, Levine, Loeblich, Weiser, and Wenrich (1964), and modified by Sprague (1966a).

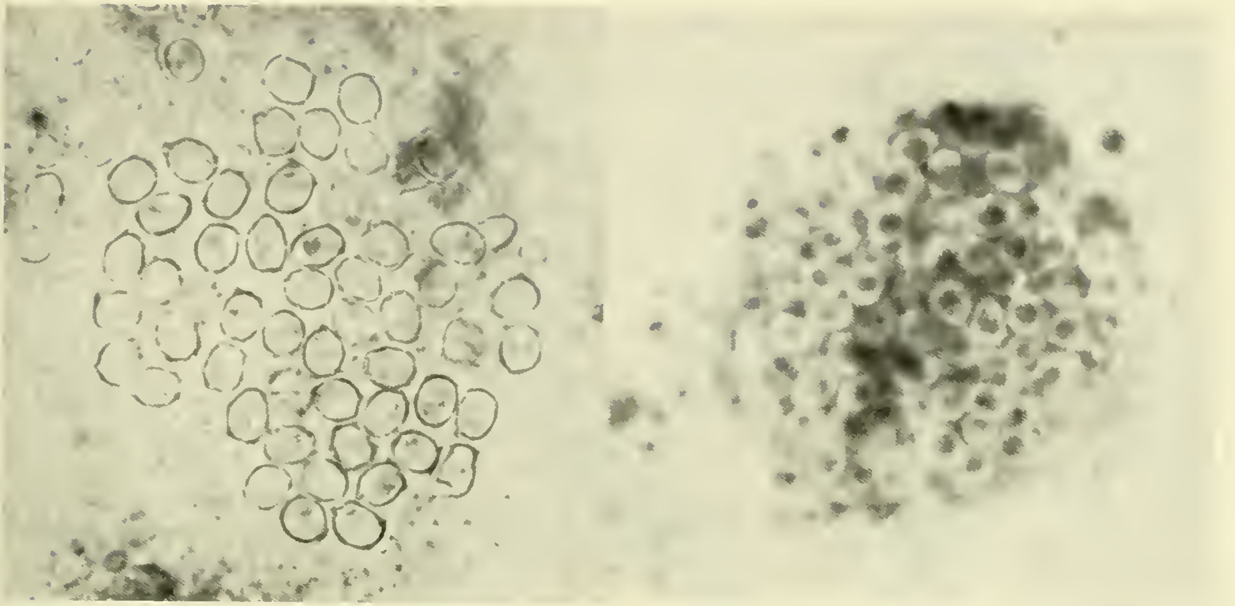

FIGURE 3.—Sporocysts of *Minchinia nelsoni* (formerly known as "MSX"), the etiolic agent of "Delaware Bay disease" in an American oyster—fresh preparation at left, and stained section at right (× 1,000).

Farley (1965), after completing a 5-year histopathological study of Chesapeake Bay oysters, categorized natural infections according to extent of invasion and nature of host response.

As an example of the effects of *M. nelsoni* on the U.S. oyster fishery, landings in New Jersey waters of Delaware Bay in the late 1940's and early 1950's had fluctuated around 6 million pounds of shucked meats until the mid-1950's, when disease decimated the stocks. Landings fell precipitously to a low of 167,000 pounds in 1960, and no significant recovery has occurred (fig. 4). Comparable effects have been felt in the high-salinity waters of lower Chesapeake Bay, another major oyster producing area.

Thus far, one alleviating influence seems to be salinity. *M. nelsoni* occurs in waters whose salinity consistently exceeds 15 o/oo; during 3 years (1963–65) of drought along the Atlantic coast, the pathogen invaded areas of middle Chesapeake Bay formerly free of the disease (Rosenfield and Sindermann, 1966). Temperature may also be important, since the pathogen appears to be quiescent during the winter.

Although several life history stages have been recognized for both species of *Minchinia*, and concurrent infections have been found (Couch, 1967b), routes of infection and methods of transmission are still unknown. Because several research groups are actively concerned with oyster diseases on the U.S. east coast, particularly with *M. nelsoni*, increased understanding of this and other pathogens should develop rapidly. Recently, we have seen in Pacific oysters from Taiwan plasmodial parasites morphologically very similar to those found in American oysters.

Léger and Hollande (1917) described another haplosporidan, *Chytridiopsis ovicola*, infecting the eggs of European oysters taken at Marennes, France. The parasite was relatively rare and occurred only in certain ovarian follicles of parasitized oysters.

Nematopsis ostrearum Prytherch, a gregarine parasite of the American oyster, was held (Prytherch, 1938, 1940) to be the cause of extensive mortalities in Virginia and Louisiana. Later studies (Sprague, 1949; Sprague and Orr, 1955) indicated, however, that *Nematopsis* did not cause deaths of oysters and suggested that *Dermocystidium* infections may have complicated earlier results. Owen, Walters, and Bregan (1952) found no correlation between *Nematopsis* infections and oyster mor-

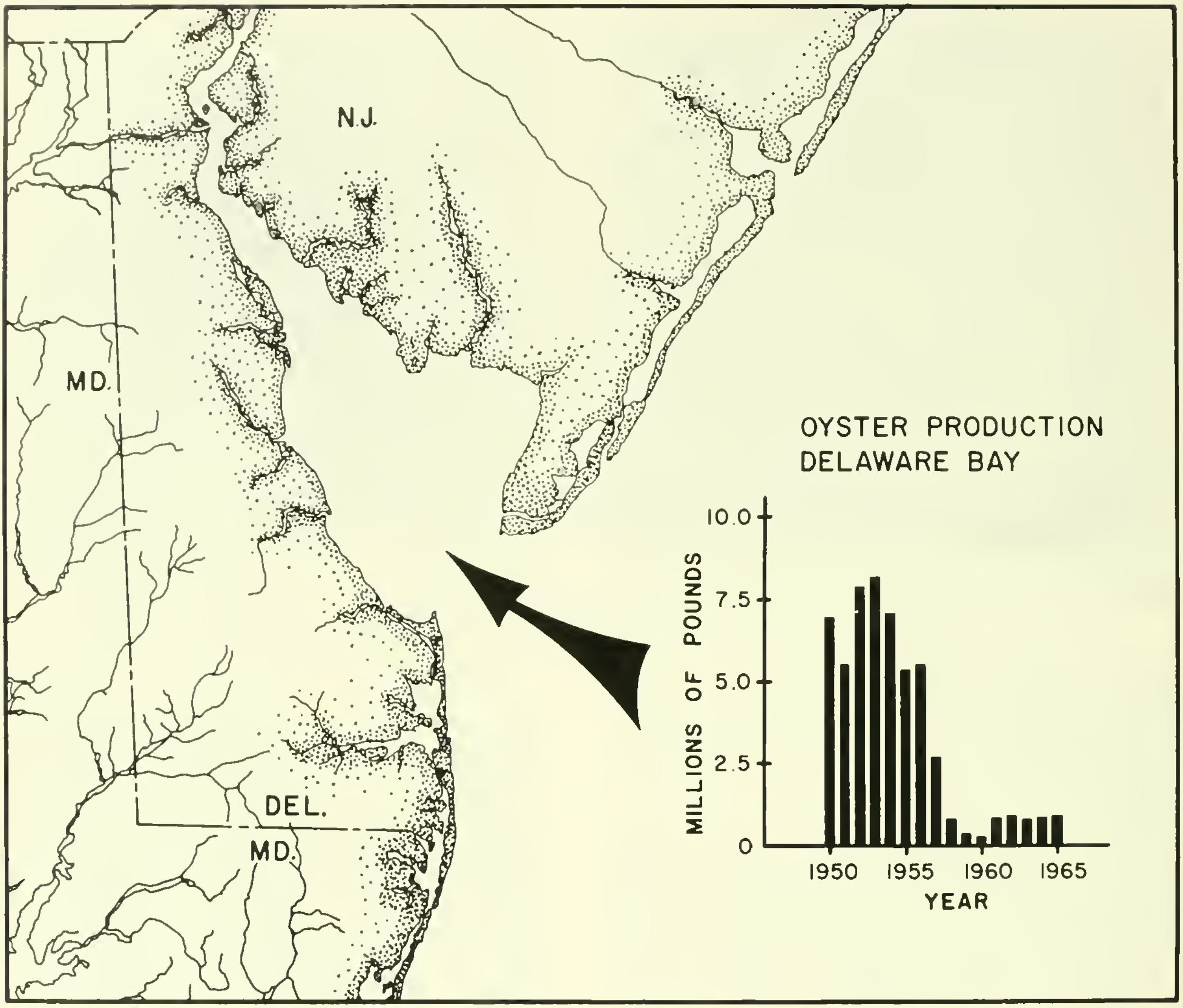

FIGURE 4.—Oyster production in New Jersey waters of Delaware Bay, 1950–65.

talities in Louisiana. Sprague and Orr (1953, 1955) demonstrated that *N. ostrearum* as described by Prytherch, was actually two species, which they designated *N. ostrearum* (emended) and *N. prytherchi*. Spores of *N. prytherchi* are larger and more elongate, localize in the gills rather than in the mantle, and have vegetative stages only in the crab *Menippe mercenaria* (Say). The life cycle of *N. ostrearum* includes a mud crab host—*Panopeus herbstii* Milne-Edwards, *Eurypanopeus depressus* (Smith), or *Eurytium limosum* (Say). In many oyster-growing areas most oysters are infected, although infections are rarely heavy. Mackin (1962) has pointed out the lack of tissue reaction to the parasite and the lack of evidence for existence of lysins or toxins. Feng (1958) found that a dynamic equilibrium existed between acquisition by the oyster of new parasites and elimination of spores.

Nematopsis was found to be widely distributed on the Atlantic and Gulf coasts of the United States by Landau and Galtsoff (1951). They found heavy infections in oysters from certain localities, such as the mouth of Chesapeake Bay, but relations with other ecological factors such as abundance of crabs were not apparent. The intensity of infection was cumulative and increased with age of the host. No evidence was obtained to indicate that *Nematopsis* infection caused poor meats or mortality of oysters.

Hexamita sp., a flagellate protozoan, occurs frequently in the digestive tract of oysters, but its parasitic or saprozoic role has not been adequately determined. First described by Certes (1882) as a commensal in European oysters, the flagellate was later held responsible for oyster mortalities from "pit disease" in Holland (Mackin, Korringa, and Hopkins, 1952). Clear evidence of pathological effects was not obtained, and heavy bacterial infections further complicated the study. *Hexamita* was also blamed for mortalities of Olympia oysters in the State of Washington (Stein, Denison, and Mackin, 1961), but again clear evidence of pathogenicity was not presented. Scheltema (1962), who examined the relation between *Hexamita* and American oysters from Delaware Bay, concluded that the organism did not contribute significantly to deaths of oysters. He suggested, as did Stein et al. (1961), that *Hexamita* may act as a pathogen during periods of low environmental temperatures and low host metabolism but that prevalence declines at higher temperatures because the processes in oysters which act to remove the trophozoites exceed the reproductive rate of the flagellate. We have recently seen *Hexamita* in Pacific oysters from Korea and Taiwan.

Several ciliate parasites have been described from American oysters. A member of the genus *Sphenophrya* was reported by the BCF Biological Laboratory, Oxford, Md. (Anonymous, 1965), as the cause of an oyster disease characterized by formation of large cysts on the gills. Richardson [2] and Laird (1961) identified ciliates in the gut of *C. virginica* from Prince Edward Island, Canada, as *Orchitophrya stellarum* Cépède. Prevalence was low, but infections were heavy and the intestinal epithelium had been invaded. *O. stellarum* is known as a serious pathogen of starfish, in which it causes gonad destruction (Cépède, 1911; Smith, 1936; Vevers, 1951). Laird speculated that the organism may be a regular and possibly harmful parasite of oysters and that starfish may become infected from them.

Mackin (1962) mentioned a ciliate parasite of oysters from the Atlantic and Gulf coasts of the United States, which he considered to be *Ancistrocoma pelseneeri*, a well-known parasite of mussels. The ciliates were abundant in the digestive tracts of oysters infected with *Dermocystidium marinum*, but Mackin did not believe that they were pathogenic to the oyster host.

Two amebae are known from American oysters. Hogue (1914, 1921) described *Vahlkampfia calkensi* and *V. patuxent*, which are parasitic in the digestive tract. She distinguished the two species on the basis of differences in the cyst wall. No evidence of pathogenicity was found, nor were these forms demonstrated to be other than saprozoic. Additional ameboid organisms isolated from American oysters were reported briefly by Sawyer (1966).

Diseases caused by Helminths

Both trematodes and cestodes parasitize oysters.

Trematodes.—European and American oysters are parasitized by larval trematodes of the genus *Bucephalus*. *B. haimeanus* was first reported by Lacaze-Duthiers (1854) from European oysters in the Mediterranean Sea, and *B. cuculus* was described by McCrady (1874) in American oysters from South Carolina. Sporocysts occur in the gonad and digestive gland of the oyster (fig. 5), and sterilize the host. The tentative life cycle of the parasite (Tennent, 1906) includes minnows (Cyprinidae) or mullets (Mugilidae) as second intermediate hosts, and gars (Lepisosteidae) as definitive hosts. Hopkins (1954, 1957b) reported parasitization of more than one-third of the oyster population in localized areas of the United States, although prevalence generally was much lower, particularly in open waters. Menzel and Hopkins (1955a, 1955b) suggested that early infections temporarily stimulate growth of the oyster, but that older infections retard growth. Hopkins (1957b) made the interesting, if somewhat facetious, observation that *Bucephalus* might be considered a gastronomically beneficial parasite in southern waters, since infected oysters have an excellent flavor and are fat-looking and glycogen-rich throughout the year, whereas normal oysters are spawned out, thin, and relatively tasteless during part of the year.

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[2] Data provided in Fisheries Research Board of Canada, Manuscript Report Series (Biology), mimeographed, unnumbered, 1939, "Report on the studies of eastern coast oysters during the season of 1939," by L. R. Richardson.

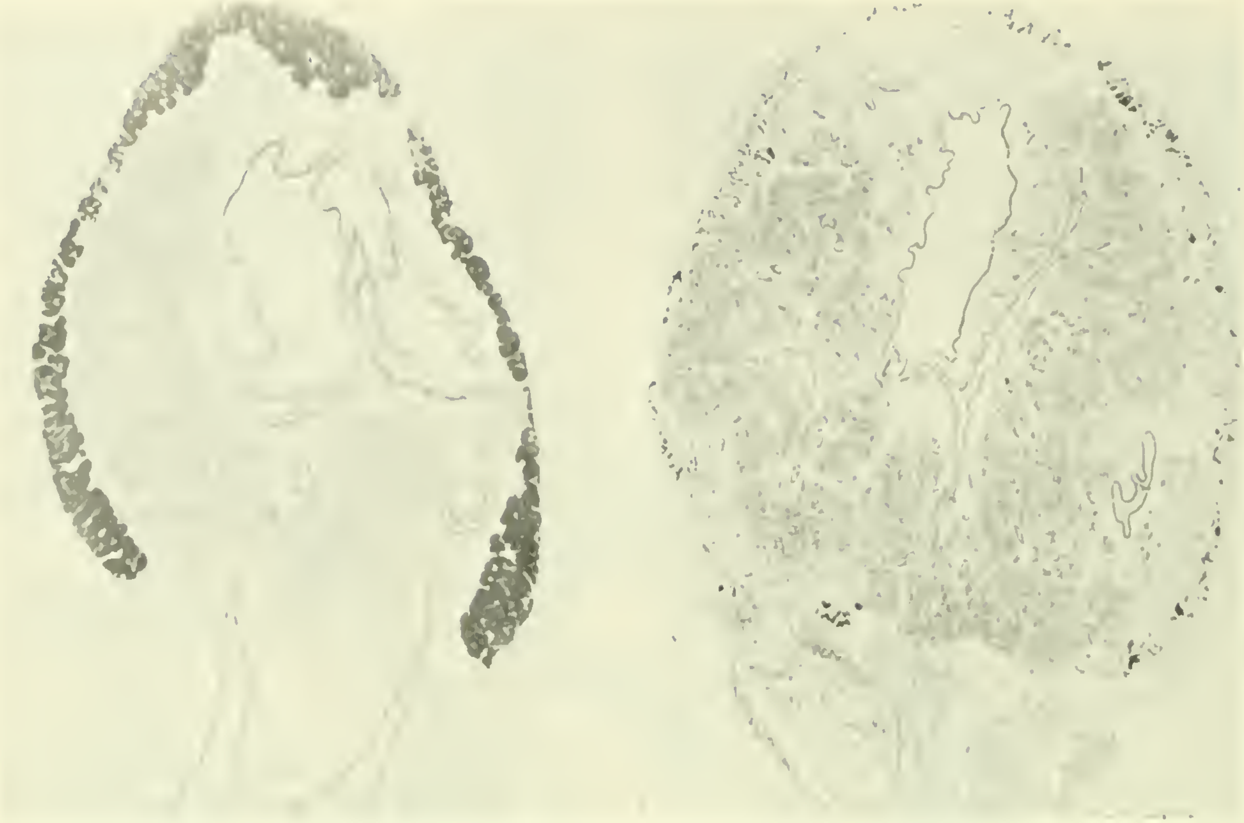

FIGURE 5.—Histological sections of oysters: (a) normal, and (b) parasitized by *Bucephalus* (× 3.5). Note in (b) the almost complete destruction of gonad tissue, which stains darkly in (a).

Recently, Cheng (1965) and Cheng and Burton (1965) used histochemical methods to examine the host-parasite relation of the American oyster and the larval trematode, *Bucephalus* sp. Parasitization caused marked changes in the distribution of fats.

Larval trematodes of the family Bucephalidae also occur in New Zealand oysters, *Ostrea lutaria* Hutton. Millar (1963) reported that oysters imported from New Zealand and maintained for breeding studies in Scotland were frequently parasitized and that the percentage mortality was much higher among parasitized individuals than among normal ones. We have recently found Pacific oysters from Taiwan to be infected with larval *Bucephalus*.

Hyperparasitization of sporocysts of *Bucephalus* in American oysters from the Gulf of Mexico was reported by Mackin and Loesch (1955). This hyperparasitization produced blackish discoloration of oyster mantle and viscera, and destruction of sporocysts, followed by release of the haplosporidan spores into host oyster tissue. Pronounced cellular reaction was elicited in the localized areas where spores were found in oyster tissue; the authors described some abnormal development of the hyperparasite in such tissue. The hyperparasite was not named, but it was considered on the basis of spore morphology to be a haplosporidan distinct from the parasite *Urosporidium pelseneeri* (Caullery and Chapellier) found in clams of the genus *Donax*.

Sprague (1964) described a microsporidan hyperparasite, *Nosema dollfusi*, of *Bucephalus* and speculated that escape of the protozoan into the tissues of the oyster could contribute to the death of the molluscan host. Shuster and

Hillman (1963) and Cheng (1964) made a similar speculation about haplosporidan hyperparasites of oysters.

Other larval trematodes occur on and in oysters. Fujita (1925, 1943) described *Gymnophalloides tokiensis*, a metacercaria which encysts, often in great numbers, on the mantle and gills. The host's physiology is disturbed, growth is halted, and reproduction is inhibited. Marine birds are definitive hosts for the parasite. Metacercariae of *Proctoeces ostrea* Fujita are also found in Japanese oysters. About 10 percent of the oysters in Hiroshima Bay were infected by the larval trematode, which localizes in gonad tissue. European oysters harbor the related *Proctoeces maculatus* Looss. Definitive hosts are labrid fishes in Europe, and snappers and red groupers, *Pagrosomus major* and *Epinephetus akaara*, in Japan.

Massive invasion by metacercariae in American oysters from the Texas coast was reported recently by Little, Hopkins, and Schlicht (1966). Feeding experiments showed that the trematodes were *Acanthoparyphium spinulosum* (Johnston), which matures in the intestine of shore birds. Most of the oysters examined had metacercariae in the mantle; the number averaged 45 worms per oyster.

Cestodes.—Oysters in several regions of the world are parasitized by larval cestodes of the genus *Tylocephalum*. These parasites are Lecanicephaloidea that occur as adults in the digestive tracts of elasmobranchs. Sparks (1963) reported heavy infections of *Tylocephalum* in American oysters introduced in Hawaii. In an addendum, Sparks noted that oysters from Florida had been reported by the BCF Biological Laboratory, Oxford, Md., to harbor similar larval cestodes (fig. 6). We have found similar larvae in oysters from Georgia and North Carolina. The coracidium of *Tylocephalum* was recently reported in the stomach and gills of American oysters collected at Pearl Harbor, Hawaii (Cheng, 1966). Penetration of gill or digestive epithelium was postulated from study of histologic sections. The pronounced cellular reaction in the subepithelial tissues—including encapsulation of the larvae—was described. Larval cestodes, probably *Tylocephalum*, have been found in Pacific oysters from Japan and Taiwan by staff members of the BCF Biological Laboratory, Oxford, Md. Members of this tapeworm group are known as parasites of pearl oysters in the Far East and were held to be the cause of pearl formation (Herdman, 1904; Herdman and Hornell, 1906; Shipley and Hornell, 1904, 1906; Southwell, 1924). Jameson (1912) presented convincing evidence, however, that invasion by larval trematodes, rather than larval cestodes, was more important in pearl development. Pearl formation around trematode and cestode larvae which invade the mantle and die appears to follow a similar pattern of host responses in bivalve mollusks (Wright, 1966).

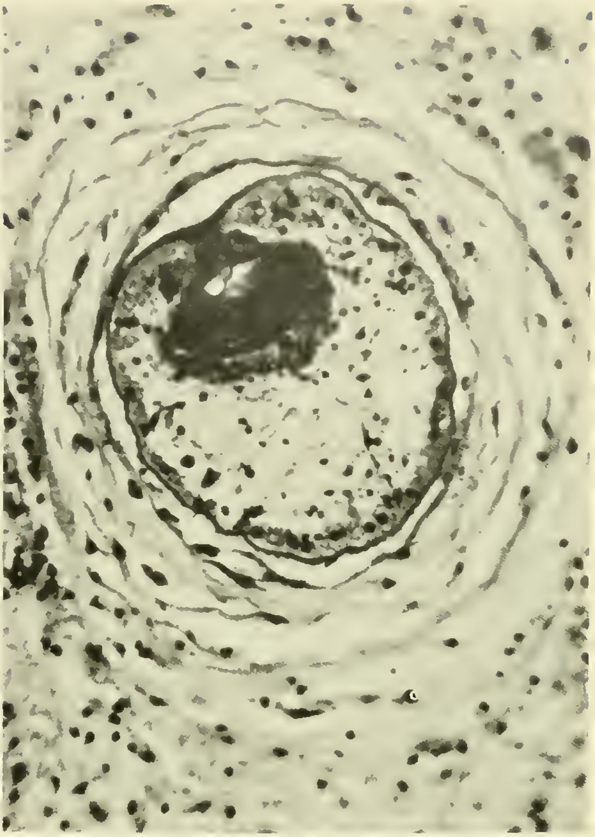

FIGURE 6.—*Tylocephalum* in American oyster from Apalachicola Bay, Fla. (× 70).

Diseases Caused by Parasitic Crustaceans

A parasitic copepod, *Mytilicola orientalis*, was described from the digestive tract of the Pacific oyster from Japan by Mori (1935). The parasite was transferred to the United States west coast with imports of seed oysters from Japan, and was described as *M. ostrea* by Wilson (1938), who was apparently unaware of Mori's report. Odlaug (1946) stated that Olympia oysters infected with even small numbers of *M. orientalis* had a lower condition index than uninfected oysters. Chew, Sparks, and Katkansky (1965) found a similar relation in Pacific oysters, and Sparks (1962) demonstrated pathological changes in gut epithelium and underlying tissues of these oysters infected with the copepod. Mori and Odlaug reported *M. orientalis* as a parasite of mussels (*Mytilus crassitesta* Lischke and *M. edulis* L.) as well as oysters, both in Japanese and United States waters. Another species, *Mytilicola intestinalis*, first described by Steuer (1902, 1903), has been blamed by Korringa (1950, 1959) and others for widespread mortalities of sea mussels, *Mytilus edulis*, in Europe but is found only rarely in European oysters (Baird, Bolster, and Cole, 1950; Hepper, 1953, 1956) and has not been reported to cause significant mortalities. A small specimen, identified as *Mytilicola intestinalis*, was found by Pearse and Wharton (1938) in an American oyster from the Florida coast. Humes (1954) believed that this copepod was probably *M. porrecta*, which he described from mussels and clams from Louisiana.

Crabs of the genus *Pinnotheres* occasionally inhabit the shell cavity of oysters, where their activities and effects suggest that they are parasites rather than commensals (Christensen and McDermott, 1958; Haven, 1959). Stauber (1945) studied a sudden increase in abundance of the oyster crab, *P. ostreum* (Say), in American oysters of Delaware Bay in 1941. He observed that the crabs robbed the oyster of food and injured the gills, resulting in a weakened condition of the host. Stauber found in 1941 that 90 percent of the oysters of Delaware Bay harbored four to six crabs in the first parasitic stage. He ascribed unusual mortalities in certain oyster populations to debilitation caused by high abundance of crabs. In 1942 abundance of crabs dropped to 25 to 30 percent, and continued to decline in following years.

Another *Pinnotheres* was described from Madagascar oysters, *Ostrea vitrifacta* Sowerby, by Poisson (1946); infestation was accompanied by development of a characteristic irritating flavor in the parasitized oyster. He speculated that this flavor might be traced in some way to the coelenterate *Sertularia*, which often grows on shells of oysters that contain *Pinnotheres*. Korringa (1952a) pointed out the striking similarity of this observation with the popular belief in Holland that eating mussels parasitized by *P. pisum* causes "nettle rash."

Tumors

Tumors in oysters have been reported. Benign mesenchymal tumors of pericardial origin have been described from oysters by Ryder (1887) and Smith (1934). The nodular, polypoid, pediculated growth found by Smith was over 3 cm. in greatest dimension. Sparks, Pauley, Bates, and Sayce (1964a) described a stalked mesenchymal tumor from the Pacific oyster that appeared to be histologically similar to that found by Smith. Sparks, Pauley, Bates, and Sayce (1964b) also reported a Pacific oyster with a tumorlike fecal impaction of unknown origin, accompanied by inflammation and encapsulation. The literature on tumors of other species of mollusks, as well as those of other invertebrates, has been reviewed by Scharrer and Lochhead (1950).

MUSSELS

Marine mussels, particularly *Mytilus edulis*, are abundant and palatable. They are grown by highly developed culture methods, especially in Western Europe. Culture of a single species, often under crowded conditions, however, increases vulnerability to disease. As with cultivated oysters, extensive and repeated mortalities, presumably caused by disease, have occurred in mussel beds. The parasitic copepod, *Mytilicola*, is the only specific pathogen that has been shown to cause mortalities in European mussels, although other parasites, particularly haplosporidan Protozoa and larval trematodes, have been reported.

Microbial Diseases

Eggs of the sea mussel from the western North Atlantic are occasionally infected with a haplosporidan, *Chytridiopsis mytilovum*. Field (1923) first described the parasite and several of its life history stages. Recently Sprague (1965b) has redescribed life history stages in more detail. The parasite has a high prevalence in some samples, although the proportion of infected eggs to normal eggs in any individual is low. Vincentiis and Renzoni (1963) recognized what seems to be the same organism in eggs of the Mediterranean edible mussel, *Mytilus galloprovincialis* L., from the Gulf of Naples. A similar parasite, *Chytridiopsis ovicola*, has been reported from eggs of the European oyster (Léger and Hollande, 1917).

Taylor (1966) described a disease of California mussels, *M. californianus* Conrad, caused by another haplosporidan, *Haplosporidium tumefacientis*. The disease, characterized by tumefactions of the digestive gland, was found in 23 of 1,114 individuals examined. The gross enlargement of the gland was apparently due to plasmodia of the parasite; no necrosis was reported. Samples of sea mussels collected simultaneously from the California coast by Taylor were not parasitized by the haplosporidan.

Sea mussels from the Baltic were found by Raabe (1934, 1936, 1938, 1949) to harbor a number of ciliates, including *Ancistrocoma pelseneeri* Chatton and Lwoff, *Kidderia mytili* (DeMorgan), *Ancistruma mytili* (Quennerstedt), and *Hypocomides mytili* (Chatton and Lwoff). The same species of ciliates have also been identified from *Mytilus* sampled in other geographic areas (Kidder, 1933; Chatton and Lwoff, 1934; Kozloff, 1946). Although many ciliates occur in bivalve Mollusca (Fenchel, 1965), a parasitic role has not been adequately determined for most of them.

Diseases Caused by Helminths

Invasion of mussels by larval trematodes is thought to be responsible in part for pearl formation. Jameson (1902) believed that most mussel pearls resulted from encystment of metacercariae and encapsulation by the host. Herdman (1904), who studied sea mussels in England, found pearls very common near Piel and attributed them to invasion by larvae of *Distomum (Gymnophallus) somateriae*.

The literature on trematode-induced pearl formation in mussels has been reviewed by Stunkard and Uzmann (1958). The relation between pearls in European sea mussels and trematode parasites was first described by Garner (1872), and later by Dubois (1901, 1903, 1907, 1909) who proposed the name *Distomum margaritarum (Gymnophallus margaritarum)* for parasites found in reddish-brown spots which served as foci for pearl formation in mussels from the French coast. Jameson (1902) stated that the larval trematodes resembled *D. somateriae* which had been described as an adult from the intestine of the eider duck, *Somateria mollissima*, by Levinsen (1881). Jameson referred the parasite to the genus *Lecithodendrium* Looss and described the process of pearl formation by the mantle of the mussel around the metacercariae. Giard (1903, 1907) confirmed these observations on pearl formation. Odhner (1905) designated the larvae causing pearl formation in mussels as *Gymnophallus bursicola*. Similar metacercariae were found by Stafford (1912) in mussels from the Gulf of Saint Lawrence. Jameson and Nicoll (1913) reviewed pearl formation in mussels and concluded that several gymnophallid larvae were involved. Since then other gymnophallid cercariae have been associated with metacercariae in mussels (Palombi, 1924; Cole, 1935; Rees, 1939). Stunkard and Uzmann (1958) fed mussels from Long Island to newly hatched eider ducks and recovered adult gymnophallids, probably *G. bursicola*.

Other larval trematodes have been described from mussels. Cole (1935) reported "orange sickness" of sea mussels at Conway in Wales. The color was due to masses of orange pigmented trematode sporocysts in the mantle and throughout the body; the tailless cercariae they contained were described as *Cercaria tenuans*. A similar condition had been noted previously by Atkins (1931a). Cole also described a second larval trematode infestation, caused by *Bucephalus mytili*. Uzmann (1953) found microcercous trematode larvae in sea mussels from Long Island and Connecticut that had a similar orange coloration. Described as *Cercaria milfordensis*, the larvae were primarily parasites of the blood vascular system of the host and had foci in the blood vessels of the mantle. Sporocyst development precluded normal gametogenesis in mussels; infected mussels held in aquaria had unusually high mortalities. Uzmann suggested that *C. milfordensis* infections are probably lethal to the host under unfavorable environmental conditions.

Diseases Caused by Parasitic Crustaceans

A well-documented example of the effects of disease on mussel populations is that of the invasion of the north European sea mussel stocks by the copepod *Mytilicola intestinalis*. A fascinating body of literature has accumulated about this parasite and its effects on mussels; only a sampling of the many published papers is cited here. Steuer (1902) first described the parasite from the intestines of Mediterranean edible mussels, and Pesta (1907) outlined the life history. Korringa (1950, 1959) described the relatively sudden appearance of *Mytilicola* in sea mussel stocks of the Netherlands in 1949 and its subsequent spread to many mussel beds during the following decade. The organism was known to occur in Mediterranean mussels since the beginning of the 20th century (Monod and Dollfus, 1932), and in 1938 was found near Cuxhaven, Germany, from whence it was assumed to have spread westward to the Netherlands. Spread was thought by Korringa and others to be aided by mussel encrusted ships, by movement of planktonic larvae, and by transfer of seed mussels from infested areas. *Mytilicola* was also very abundant in localized areas of the English coast in 1946. Korringa stated that the condition of mussels was generally correlated with intensity of parasitization; mussels with less than 5 copepods were still healthy, those with 5 to 10 were visibly thinner, and more heavily infested lots suffered serious mortalities. According to Meyer-Waarden and Mann (1954) and Mann (1956), gonad weights of infested individuals were 10 to 30 percent less than those of nonparasitized mussels.

There is some indication, however, that *M. intestinalis* exerts a less severe effect on populations of *Mytilus galloprovincialis* than on those of *M. edulis*, possibly because of its longer association with *M. galloprovincialis* and the consequent better adaptation of host and parasite—as was pointed out by Fleury, Lubet, and Le Dantec (1951). Hrs-Brenko (1964), for example, found no difference in condition index of parasitized and unparasitized mussels *(M. galloprovincialis)* on the Yugoslav Adriatic coast, and Genovese (1959) made similar findings on the Italian coast.

Infestation of sea mussels led to poor growth, thin meats (Cole and Savage, 1951; Mann, 1951), cream-colored rather than dark brown liver, failure of byssal development, and a dirty red-brown color. Reproduction of the parasite was accelerated by warm water, and the many young parasites present in the summer invaded and killed mussels. Deaths occurred among mussels of all sizes, including "seed." Mussels fell from culture racks and died during transport to markets (Brienne, 1964). Density of mussel beds was believed to directly influence survival and multiplication of the parasite. Infestations were light in areas where the mussels were thinly scattered and near the surface of the water. Because of the continued spread of *Mytilicola* in the Netherlands, an extensive scheme of repeated dredging of natural beds, transfer of lightly infested stocks, and destruction of heavily infested stocks was outlined by Korringa (1959) to create a barrier to further invasion.

Mytilicola in mussel populations grown on floats in Spain was studied by Andreu (1963). He found the infestation to be greater near shore where tidal currents were weak. Vertical distribution of the parasite in cultured mussels grown on 6–m. ropes was uniform in areas of strong currents but increased with depth where currents were weak. Such findings agree well with those of Hepper (1955), who concluded from field observations that mussels raised from the bottom, or in fast-moving water at either end of an estuary, were less heavily infested with *Mytilicola* than those on the bottom, in slow-moving water, or in the midregions of estuaries. Hepper felt that control of the copepod was possible by using off-bottom culture or by locating culture beds in fast-moving water or at the brackish-water ends of estuaries.

M. intestinalis, except for one doubtful North American record (Pearse and Wharton, 1938), is known only from Europe. It has been reported from Germany (Caspers, 1939; Meyer and Mann, 1950, 1952a, 1952b; Meyer-Waarden and Mann, 1956), the Netherlands (Korringa, 1951b, 1952b, 1953, 1957a), Belgium (Leloup, 1951, 1960), Scotland, England, and Ireland (Ellenby, 1947; Grainger, 1951; Hockley, 1952; Thomas, 1953; Bolster, 1954; Waugh, 1954), the north coast of France (Dollfus, 1914, 1927; Monod and Dollfus, 1932; Brienne, 1964), the northwest coast of Spain (Andreu, 1960, 1961, 1963), the Mediterranean Sea (Bassedas, 1950; Meyer-Waarden and Mann, 1953), and the Adriatic Sea (Steuer, 1902; Pesta, 1907; Meyer-Waarden and Mann, 1953). Waugh (1966) has mapped the recent distribution of the parasite in northern Europe. A conference to review and discuss problems of parasitization by *Mytilicola* was held in Paris, and the proceedings were published in 1951 (Cole, 1951a; Dollfus, 1951; Havinga, 1951; Heldt, 1951; Korringa, 1951b; Korringa and Lambert, 1951; Lambert, 1951a, 1951b; Leloup, 1951; Meyer and Mann, 1951). It was agreed that *Mytilicola* constituted a severe threat to the mussel industry of Europe, but whether the copepod was a direct or indirect cause of death was left undecided. Continuing mortalities associated with the presence of *Mytilicola* (Brienne, 1964), however, indicate a causal relationship, possibly influenced by stresses of spawning, high temperatures, and inadequate food supply.

Another species, *Mytilicola porrecta* Humes, occurs in ribbed and recurved mussels (*Modiolus demissus* Sowerby and *Mytilus recurvus* Rafinesque) in the Gulf of Mexico. Humes (1954) found as many as 15 individuals per mussel, but no pathology or mortality was indicated. A third species, *Mytilicola orientalis*, known to occur in *Mytilus edulis* and *M. crassitesta*, was recently reported from the California mussel by Chew, Sparks, and Katkansky (1964).

Pinnotherid crabs of several species, best known as parasites of oysters, also occur in mussels. McDermott (1962) found that *Pinnotheres ostreum* and *P. maculatus* cause gill damage and palp erosion in *M. edulis*. Earlier, Atkins (1931b) described similar palp abnormalities in mussels from England.

CLAMS

Many species of bivalves called by the general term "clam" are harvested throughout the world. Some species constitute a significant commercial crop in many coastal areas; other species are fished for sport or are ignored. Changes in clam abundance have been documented, although mass mortalities comparable to those in oysters and mussels have not been reported. Mass deaths may pass unnoticed in sediment-hidden clams; it may be for this reason that information on diseases of clams is scarce. Among the diseases and parasites that are known in clams are: several protistan organisms, larval trematodes, larval cestodes, parasitic copepods, and tumors.

Microbial Diseases

Coe's (1955) study of population fluctuations of the California bean clam, *Donax gouldi* Dall, included a description of a possible fungus parasite "apparently similar to *Dermocystidium marinum*" as a cause of mass mortalities during the summer. Moribund clams of all ages were heavily infected with "irregularly spherical or ovoid cells, 2 to 6 microns in diameter." The identity of the pathogen was not further determined, however, and the information presented is insufficient to identify it as a *Dermocystidium*.

Much earlier, Léger (1897) found a coccidian, *Hyaloklossia pelseneeri*, in kidneys of *Donax* sp. and *Tellina* sp. in Europe, and Léger and Duboscq (1917) described another coccidian, *Pseudoklossia glomerata*, parasitic in *Tapes floridus* L. and *T. virgineus* L. from the Mediterranean Sea.

Ciliate parasites have been described from soft-shell clams, *Mya arenaria* L., by Uzmann and Stickney (1954). The peritrich *Trichodina myicola* Uzmann and Stickney was found, often in large numbers, on the palps. These infections were often accompanied by the nonpathogenic thigmotrich *Ancistrocoma myae* (Kofoid and Busch). *A. myae* had been described earlier from *M. arenaria* sampled in California (Kofoid and Busch, 1936; Kozloff, 1946) and in Massachusetts (Chatton and Lwoff, 1950). Kozloff considered the ciliate identical to *A. pelseneeri*, a common parasite of sea mussels. Fenchel (1965) also found *Ancistrocoma myae* in nearly 100 percent of *M. arenaria* sampled from two locations in Denmark.

Diseases Caused by Helminths

Several life history stages of diverse trematodes occur in the soft-shell clam. Uzmann (1952) reported sporocysts and cercariae *(Cercaria myae)* from gonads and digestive gland of this clam from Massachusetts, and held that parasitization resulted in a condition known as "water belly." (Subsequent observations, summarized by Dow and Wallace (1961), suggest that this condition may be a general sign of physiological disturbance.) Uzmann considered *C. myae* to be the same species as that reported by Stafford (1912) from the soft-shell clam in the Gulf of Saint Lawrence. Hutton (1953) believed that the larvae were members of the genus *Gymnophallus.* Stunkard and Uzmann (1958) discussed gymnophallid sporocysts and cercariae from the soft-shell clam, and Stunkard (1960) found echinostome metacercariae of the genus *Himasthla* in palps and gills of clams from the Maine coast. Three species were recognized. Earlier, Stunkard (1938) had demonstrated experimentally that cercariae of *Himasthla* would penetrate and encyst in the gills of *Mya arenaria* and a number of other bivalves, and Uzmann (1951) had reported natural occurrence of *Himasthla quissetensis* (Miller and Northrup) in *M. arenaria.* Susceptibility and response of a number of marine pelecypods, including four species of clams, to cercariae of *H. quissetensis* was tested experimentally by Cheng, Shuster, and Anderson (1966). Metacercariae were found in all clams and mussels but not in oysters used in the study.

Several larval trematodes have been reported from clams of the genus *Donax*. Giard (1897, 1907) identified bucephalid and gymnophallid cercariae. Rees (1939) found gymnophallid metacercariae, and Young (1953) described the life cycle of a monorchid, *Postmonorchis donacis,* whose larvae occur in the California bean clam. Hopkins (1958) identified sporocysts and cercariae of three species, and metacercariae of two species, in coquina clams, *Donax variabilis* Say, from the Texas coast. Infections by larval trematodes were considered by Pelseneer (1896, 1906, 1928) to be responsible for reduced abundance of *Donax vittatus* in France, and Coe (1946) held that trematode parasites (probably *Postmonorchis donacis*) were important in controlling population size in California *Donax gouldi.*

Fujita (1906, 1907, 1943) has described two larval trematode parasites of asari clams, *Tapes philippinarum* Adams and Reeve, from Japan. Parasitic castration of the hosts was observed.

Hopkins' (1957a) brief but excellent exposition of the role of parasitism in marine communities referred to an interesting interrelationship of host, parasite, and hyperparasite in the case of *Donax trunculus* parasitized by trematodes, which in turn were parasitized by the haplosporidan *Urosporidium pelseneeri* (Caullery and Chappellier). The often severe fluctuations in abundance of this clam have been attributed to shifts of balance in this tripartite relationship (Caullery and Chappellier, 1906; Cépède, 1911). Other haplosporidan and microsporidan hyperparasites of *Donax* have also been described (Guyénot, Naville, and Ponse, 1925; Dollfus, 1946; Mackin and Loesch, 1955).

MacGinitie and MacGinitie (1949) surveyed a number of species of clams from the Pacific coast of the United States for parasitization by larval tapeworms. Encysted larvae of the cestode genus *Anabothrium* were found, occasionally in large numbers, in the foot muscles of the gaper clam, *Schizothaerus nuttallii* Conrad. The definitive host of the *Anabothrium* sp. found in clams was identified by MacGinitie and MacGinitie as the bat stingray, *Myliobatis californicus.*

Sparks and Chew (1966) described remarkable levels of parasitization of littleneck clams, *Venerupis staminea* (Conrad), from Humboldt Bay, Calif., by larval tetraphyllidean cestodes of the genus *Echeneibothrium.* Cysts of the worm were closely packed throughout the tissues of the clams, which were abnormally exposed on the surface of gravel beds. Adult *Echeneibothrium,* with bothridia similar to those of larvae in clams, were found in bat stingrays caught in the same area.

Diseases Caused by Parasitic Crustaceans

Clams, like certain other bivalves, harbor parasitic copepods. Hoshina and Kuwabara (1959) described *Mytilicola mactrae* from Japanese *Mactra veneriformis* Reeve. About half the clams in a sample of 69 were infested. Yamaguti (1939) described another species from *Brachidontes senhausi* (Reeve), and Humes (1954) found *M. porrecta* in a single hard clam, *Mercenaria mercenaria* (L.), from the Gulf of Mexico.

Tumors

Hueper (1963) reported cauliflowerlike papillary tumors at the anterior end of soft-shell clams collected from Chesapeake Bay. He termed the condition "endemic" and reported it in about 2 percent of clams collected from certain bay areas.

OTHER BIVALVE MOLLUSKS OF COMMERCIAL IMPORTANCE

There are two other groups of commercially important bivalve mollusks—scallops and pearl oysters—for which some information on diseases and parasites is available. Mass mortalities caused by disease have not been reported in either group. Scallops are infected by protozoan and trematode parasites, and occasionally are affected by a shell disease. Pearl oysters harbor a number of larval trematode parasites.

Scallops

Although major mortalities have occurred in scallop populations (Dickie and Medcof, 1963; Medcof and Bourne, 1964; Merrill and Posgay, 1964; Sanders, 1966), none has been definitely associated with disease. In fact, only a few diseases and parasites are known, and their effects on the hosts are slight.

Two parasites of scallops have been recognized. A coccidian, *Pseudoklossia pectinis*, was described as a rare parasite in the kidney tubules of the great scallop, *Pecten maximus*, at Roscoff, France, by Léger and Duboscq (1915b), who found usually light infections with no extensive pathology. Sporocysts and fork-tailed cercariae of a trematode (not further identified) were found by Linton (1915) in large bay scallops, *Aequipecten irradians*, from Woods Hole, Mass. Infections were rare.

An abnormal brown discoloration of meats was studied by Medcof (1949) in sea scallops, *Placopecten magellanicus* (Gmelin), off the south coast of Nova Scotia, Canada. He considered the condition to result from extensive invasion of the shell by a boring sponge. In advanced stages, the shell was completely honeycombed, causing excessive inner shell deposition and producing weak shrunken individuals which, Medcof assumed, died eventually from effects of the shell disease. Meat yields from heavily infected scallops were less than half those of normal individuals, but only older scallops (8 or 9 years old) were infected.

Pearl Oysters

Pearl-producing bivalves of the family Pteriidae, called "pearl oysters" but actually taxonomically remote from edible oysters of the family Ostreidae, occur in many parts of the world (Sivalingam, 1962). Interest in parasites of pearl oysters has naturally centered on those larval worms considered responsible for pearl formation (Jameson, 1902, 1912; Wright, 1966), but a few other parasites and diseases have been recognized.

Parasites of the pearl oysters of Ceylon, *Margaritifera (Pinctada) vulgaris* Schum., were studied by Shipley and Hornell (1904) and Southwell (1911, 1912) particularly with regard to the role of parasitic worms in pearl formation. These authors described several stages of cestode larvae, some clearly trypanorhynchid, from the digestive gland and gills of the pearl oyster. The worms occurred, often in great numbers, in fibrous capsules. Several larval trematodes were also found, but only one, described as *Muttua margaritiferae*, occurred in abundance. Metacercariae localized in the gills. Other metacercariae, described as *Musalia herdmani*, were found in the muscles, mantle, and foot. An aspidobothrid trematode, *Aspidogaster margaritiferae*, occurred in the pericardial cavity, and several species of encysted larval nematodes were seen in the gonads, stomach walls, and adductor muscles.

Pearl oysters of Japan, *Pinctada martensii*, are commonly infested with sporocysts and cercariae of a bucephalid trematode described as *Bucephalus margaritae* by Ozaki and Ishibashi (1934). Experimental infections of several species of small fishes with cercariae from pearl oysters (Sakaguchi, 1962, 1966a) produced metacercariae morphologically the same as those identified as *B. varicus* by Manter (1940). Adult trematodes were found in the digestive tracts of carangid fishes, *Caranx sexfasciatus* and *C. ignobilis*, which were abundant in the waters near oyster farms where pearl oysters were heavily infested (Sakaguchi, 1966b). Marked decline in condition of pearl oysters resulted from invasion by larval trematodes. Sporocysts were found to overwinter in the host, and cercarial production began again when water temperatures rose in spring (Sakaguchi, 1965). Pearl oysters infected in the preceding year suffered high mortalities after insertion of pearl cores, and high percentages of pearls produced by infected individuals were of low quality (Sakaguchi, 1964).

DISEASES OF CRUSTACEA

Crustacea such as crabs, lobsters, and shrimps are among the most valuable of marine crops in many parts of the world. Large populations of crustaceans occur on the continental shelves, and often part or all of the life cycle is spent in estuarine or inshore waters. Here individuals may be observed and studied in natural habitats as well as in the landed catches. These studies have disclosed certain parasites and diseased conditions. Disease may have severe effects on survival, particularly when crabs and lobsters are impounded before sale. Diseases exist in natural populations of Crustacea as well, although effects are less apparent than in captives or in more sedentary marine animals. No widespread epizootic is known for marine Crustacea that would be comparable to "krebspest," a fungus disease that swept through populations of freshwater crayfishes of Europe (Schikora, 1906, 1926; Schäperclaus, 1935; Nybelin, 1935; Mannsfield, 1942).

CRABS

Many species of crabs have great commercial value in various parts of the world. Consequently, diseases and parasites have been included in studies of factors which affect abundance. Microbial diseases, helminths, and parasitic crustaceans occur in crabs.

Microbial Diseases

Among the microbial diseases of crabs are those caused by a virus, several fungi, bacteria, and a variety of protozoans.

Viruses.—Virus diseases have not been reported from marine invertebrates, with the exception of one described recently, and only very briefly, by Vago (1966), in swimming crabs, *Portunus depurator* (L.), from the French Mediterranean coast. Gross disease signs included the slow development of paralysis, and sometimes a slight darkening (presumably of the exoskeleton) in later phases of the disease. Virus particles were seen with the electron microscope; inoculation of blood from infected animals produced disease signs in healthy crabs; and infections were obtained with ultrafiltrates and ultracentrifugates of homogenized tissues from sick crabs. No indication of disease prevalence was given by Vago.

Recently, Sprague and Beckett (1966) have published a preliminary note on a disease of soft-shell and molting blue crabs, *Callinectes sapidus* Rathbun. The disease, of undetermined but possibly viral etiology, was called "gray crab disease." It occurred in crabs from seaside bays of Virginia, where it apparently caused some deaths among captive crabs.

Bacteria.—King crabs, *Paralithodes camtschatica* (Tilesius) and *P. platypus* Brandt, from the eastern North Pacific are occasionally affected by "rust disease," which seems to result from action of chitin-destroying bacteria on the exoskeleton. Microorganisms of this type are common in the sea (ZoBell and Rittenberg, 1938; Hock, 1940, 1941) but usually degrade the exoskeletons of dead animals and do not affect living individuals. Over thirty species of chitin-destroying bacteria are known, of which half have been isolated from shells of crustaceans.

Bright, Durham, and Knudsen[3] described observations of rust disease in landed catches of king crabs from Kachemak Bay, Cook Inlet, Alaska, as well as experimental studies of the bacteria involved. The disease was characterized by progressive darkening and softening of the exoskeleton, particularly on the ventral surfaces. Underlying living tissues were unaffected. Natural infections reached 11 percent in larger older crabs in 1957 but were much lower in 1958 and 1959. Shell abrasions and injuries served as foci of the disease, which developed experimentally within 2 weeks. The disease was not carried over to the new exoskeleton after molting, but recently shed crabs were highly susceptible because the new shell was easily punctured or abraded. Chitin-destroying bacteria were isolated from infected crabs, and cultured organisms produced the disease experimentally in normal crabs. Similar bacteria were also isolated from sea water in Kachemak Bay. The authors concluded that the disease would not affect the commercial fishery seriously unless the catch of crabs was substantially less than annual recruitment, since larger individuals, which do not molt annually, were more frequently infected.

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[3] Data furnished from unpublished contract report, "King crab investigations of Cook Inlet, Alaska," by Donald B. Bright, Floyd E. Durham, and Jens W. Knudsen of the Allan Hancock Foundation, University of Southern California, Los Angeles, to BCF Biological Laboratory, Auke Bay, Alaska, June 1960. (Cited with permission of Laboratory Director, BCF Biological Laboratory, Auke Bay, Alaska.)

Fungi.—Eggs of blue crabs from lower Chesapeake Bay were found to be parasitized by a fungus *Lagenidium callinectes* Couch (Couch, 1942; Sandoz, Rogers, and Newcombe, 1944; Sandoz and Rogers, 1944; Newcombe and Rogers, 1947; Rogers-Talbert, 1948). Infected eggs either failed to hatch, or gave rise to abnormal zoea larvae. Infection levels were as high as 90 percent of a sample of ovigerous female crabs, and up to 25 percent of the eggs in a "sponge" (egg mass). Penetration of the egg mass was slow and did not exceed 3 mm. This fact, combined with the short (2-week) incubation time, permitted normal development of much of the egg mass internal to the infection. Experimentally, the fungus developed normally in salinities from 5 to 30 o/oo. The fungus was transmitted experimentally to the eggs of two other species of crabs (the oyster crab and the mud crab, *Neopanope texiana* Rathbun) inhabiting the same Bay area.

Pea crabs *(Pinnotheres)* taken from the sea mussel at Plymouth, England, were parasitized by the fungus *Leptolegnia marina* (Atkins, 1929, 1954a). The mycelium was usually found in the gills but penetrated other body organs and appendages as well. Zoosporangia developed in the appendages, and large numbers of zoospores were released upon the death of the host. No further growth of the fungus took place in dead crabs, and no external development, beyond papillae of zoospore exit tubes, was seen. Atkins (1954b, 1955) described two other fungi, *Plectospira dubia* and *Pythium thalassium*, which infect eggs of pea crabs and other Crustacea.

Protozoa.—Gregarines are common parasites of many Crustacea, and an extensive and at times confusing literature has accumulated. Many members of the group have been reported from crabs. For example, species of the genus *Cephaloidophora* occur in spider and fiddler crabs of the United States east coast (Watson, 1915, 1916a, 1916b; Kamm, 1922), in the striped shore crab, *Pachygrapsus crassipes*, of the Pacific coast, and in the Mediterranean "flat crab," *Pachygrapsus marmoratus* (Ball, 1938; Théodoridès, 1961, 1962). As mentioned in the discussion of oyster diseases, several representatives of the genus *Nematopsis* occur in Atlantic species of mud crabs (Prytherch, 1940; Ball, 1951; Sprague and Orr, 1955). Although the gregarines are not usually considered serious pathogens of Crustacea, Ball pointed out that masses of the parasites may occlude the lumen of the intestinal caeca and may cause sloughing or thinning of the epithelium.

Several microsporidans are parasites of crabs. Sprague (1965a) described a species of *Nosema* parasitic in muscles of the blue crab. Infected muscles became opaque with a coarse fibrous texture, and heavy infections caused lysis of myofibrils. He considered the parasite to be common and widespread in Chesapeake Bay, and believed it might be a significant factor in crab mortality. Sprague (1966b) also described *Plistophora cargoi* from the skeletal and cardiac muscles of a single blue crab from the Patuxent River, Md. Earlier, Perez (1905a, 1905b) reported *Nosema pulvis* in the muscles of the green crab, *Carcinus maenas* (L.), and Perez (1907) also described ovarian infections with a microsporidan, *Thelohania maenadis*, in green crabs from Arcachon, France. The parasite normally occurred in the body muscles.

Ciliates are also significant parasites of crabs. Serious mortalities of molting blue crabs from Chesapeake Bay occurred in the summers of 1965 and 1966. Their gills had a massive infestation of peritrichous ciliates (fig. 7) of the genera *Lagenophrys* and *Epistylus* (Couch, 1966, 1967a). Mortalities were most severe among crabs in holding tanks just before or after molting, but wild crabs were also heavily infested, and fishermen reported mortalities. Infestations of gills frequently seemed heavy enough to interfere with respiration.

Another ciliate, *Anophrys sarcophaga* Cohn, is found in the blood of green crabs. Originally described as a free-living form (Cohn, 1866), it was first seen in the blood of crabs by Cattaneo (1888). Poisson (1930) described the

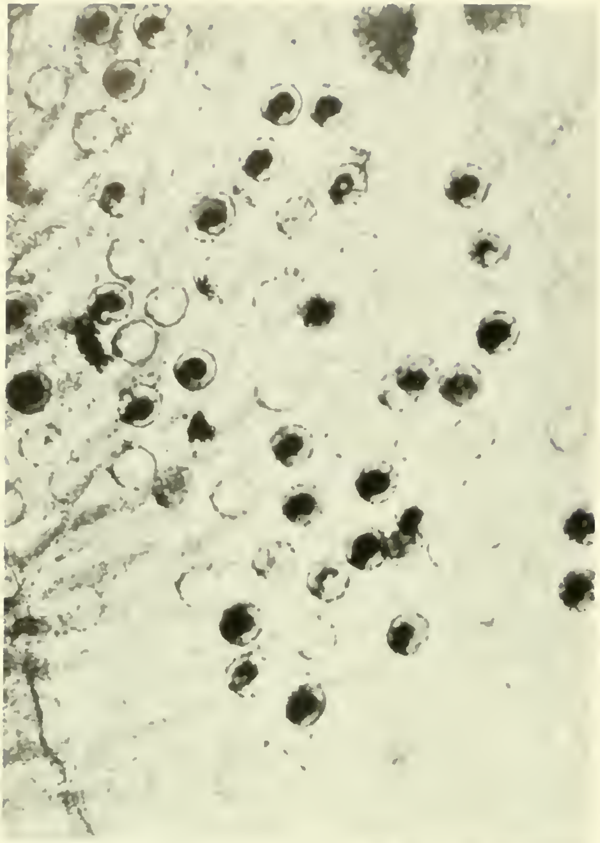

FIGURE 7.—*Lagenophrys* encysted on gills of blue crab (× 70).

active and encysted forms of the parasite in great detail. He also cultured the organism. *Anophrys* apparently ingests large numbers of host amebocytes, and multiplies until the blood becomes a dense "soup" of motile parasites. The disease, though often fatal once infection occurred, was relatively rare on the French coast. Experimental infections, achieved by injecting the ciliates, killed crabs in 2 to 7 days. Certain individual crabs seemed resistant to infection, but no antibody response was detected. Effects on the parasites included inhibition of reproduction, immobilization, and eventual death.

Diseases Caused by Helminths

Helminth infestations include larval trematodes and cestodes, as well as nemerteans and leeches.

Trematode metacercariae are common in several species of crabs. Larvae of *Microphallus* (*Spelotrema*) *nicolli*, encysted in body muscles of blue crabs, were described by Cable and Hunninen (1940). Adult trematodes occur in young herring gulls, *Larus argentatus*, and sporocyst generations in the snail *Bittium alternatum* (Say). A haplosporidan hyperparasite, *Urosporidium crescens* [De Turk], has been found in metacercariae of *Microphallus nicolli* from blue crabs caught in North Carolina (Anonymous, 1940). One third of the crabs examined contained metacercariae, but the extent of hyperparasitization was not determined. The host metacercarial tissue was often completely destroyed, leaving little more than a sack of protozoan spores. Invasion by *Urosporidium* was thought to occur before encystment of cercariae. Masses of dark pigmented spores in the destroyed metacercaria produce a black spot, which has led to the application of the descriptive colloquial term "pepper crab" to hyperparasitized individuals. "Pepper spots" occur most commonly in fat bodies, digestive gland, and muscles of the crab.

Metacercariae of *Microphallus* (*Spelotrema*) *carcini* Lebour were reported from the hepatopancreas of green crabs from the English Channel (Guyénot et al. 1925), the Mediterranean (Timon-David, 1949), and elsewhere. Hyperparasitization of metacercariae by the microsporidan *Nosema (Plistophora) spelotremae* was reported by Guyénot et al. Metacercariae of *Microphallus similis* (Jägerskiöld) occur in the hepatopancreas of the green crab of the western North Atlantic (Stunkard, 1957). Young green crabs were killed in 10 to 20 days by massive experimental exposure to cercariae of *M. similis*.

Larval diphyllidean cestodes (*Echinobothrium affine* Diesing) have been reported by Dollfus (1964a, 1964b) from green crabs sampled at Roscoff on the coast of France.

Juvenile nemerteans, *Carcinonemertes carcinophila* (Kölliker), encyst on the gills of the blue crab. After the female crab spawns, the worms excyst and migrate to the egg mass, where they mature, lay eggs, then return to the gills (Davis, 1965). Hargis (1959) has cited this parasite as an indicator of host physiology, since Hopkins (1947) pointed out that increased size and more noticeable color were characteristic of reencysted worms after the host has spawned. This and other nemerteans have been described from a number of crabs, including the green crab, of Europe (Coe, 1902; Humes, 1942).

A localized mortality of blue crabs, thought to be caused by parasitization by leeches, *Myzobdella lugubris* Leidy, was reported from a Florida river by Hutton and Sogandares-Bernal (1959). A sample of 7 crabs had 32 leeches attached near the base of the legs and near perforations in the exoskeleton. The parasite is known from the Atlantic and Gulf coasts of the United States but had not previously been considered to cause mortalities (Moore, 1946).

Other leeches occur on crabs. Oka (1927) described *Carcinobdella kanibir* from Japanese edible crabs, *Chionoecetes opilio*. Egg cases and adults of the leech *Notostomobdella cyclostoma* (Johansson) are common on Alaska king crabs, particularly during summer (Moore and Meyer, 1951; Bright et al., see footnote 3). Undescribed worms, probably leeches, were seen by MacKay (1942) on the abdomens of female Dungeness crabs, *Cancer magister* Dana, from British Columbia. The worms were much larger on egg-bearing crabs and were found chiefly among the eggs.

Diseases Caused by Parasitic Crustaceans

Parasitic crustaceans—rhizocephalans, isopods, and copepods—also infest crabs.

Many species of crabs, in many parts of the world, are parasitized by rhizocephalan Cirripedia. These parasites invade the host's body and cause degeneration of the gonads (Reinhard, 1956). The tumorlike body of the rhizocephalan ramifies throughout much of the crab and causes extensive morphological changes. The crab is usually sterilized, secondary sex characters are modified, and molting is often inhibited (Giard, 1888; Potts, 1906; Smith, 1906; Cantacuzène, 1925; Reinhard, 1950; Ichikawa and Yanagunachi, 1957).

Brachyuran or true crabs are parasitized by members of the rhizocephalan family Sacculinidae. In U.S. waters, crabs most frequently parasitized are the green crab of the Atlantic coast, and the masking crab, *Loxorhynchus grandis*, the kelp crab, *Pugettia producta* (Randall), and the black-clawed crab, *Lophopanoepeus bellus* (Stimpson) of the Pacific coast. Green crabs and swimming crabs, *Macropipus* (*Portunus*) *holsatus* (Fabricius), from the English coast are parasitized by *Sacculina carcini* Thompson (Delage, 1884; Day, 1935; Foxon, 1940). Blue crabs from the Gulf of Mexico are parasitized by the rhizocephalan *Loxothylacus texanus* (Hopkins, 1957a). Mud crabs, *Eurypanopeus depressus* (Smith), from lower Chesapeake Bay (Virginia) were discovered by Van Engel, Dillon, Zwerner, and Eldridge (1966) to have high incidences of the sacculinid *Loxothylacus panopaei* (Gissler). The localized nature of the infestations suggested that the parasite had been introduced with its hosts in shipments of oysters from the Gulf of Mexico.

Many species of anomuran crabs may be parasitized by rhizocephalans. King crabs, *Paralithodes platypus*, from Alaskan waters are occasionally invaded, probably by a species of *Peltogaster* (J. B. Kirkwood, written communication, April 14, 1967). Hermit crabs are also frequently invaded by members of the family Peltogastridae. Reinhard (1942), who examined 3,092 *Pagurus pubescens* Kroyer from the Maine coast of the United States, found 13.7 percent parasitized by *Peltogaster paguri* Rathke. The same rhizocephalan occurs on the coast of France, where its host is *Pagurus bernhardus* (L.) (Perez, 1927, 1928, 1931a, 1931b, 1931c). Infestation can have significant effects on crab populations, since parasitization usually causes degeneration of host gonads. Perez (1929, 1931a), however, found interesting evidence for sterilization and mortalities of *Peltogaster paguri* because of hyperparasitization by the epicaridean isopod *Liriopsis pygmaea* (Rathke); in some samples from northern France, most of the rhizocephalans were parasitized. Perez believed that this parasitization was an important control for *Peltogaster* populations.

Epicaridean isopods can also be significant parasites of crabs. Two families are of importance: the Bopyridae, which live principally in the gill chambers, and the Entoniscidae, which invade the haemocoele. In some species morphological modification for parasitic existence parallels that in rhizocephalans (Veillet, 1945). Effects on the crab host often include sterilization and changes in secondary sexual characteristics (Tucker, 1930; Reverberi, 1943, 1952;

Reinhard and Buckeridge, 1950). Parasitization of crabs by female entoniscids causes internal deformities, including reduction in size of organs (Atkins, 1933; Reinhard, 1945) and changes in the nervous system (Matsumoto, 1953).

Copepods are known as parasites of crab eggs. Connolly (1929) described *Choniosphaera cancrorum* from the egg masses of the American rock crabs, *Cancer borealis* and *C. irroratus*. Johnson (1957) found the same species on green crabs from the Maine coast. Gnanamuthu (1954) described *Choniosphaera indica* from gills and egg masses of an Indian edible crab, *Neptunus sanguinolentus*. Copepod larvae were found between the crab's gill lamellae, probably feeding on tissue fluids; adults apparently suck fluids from the crab eggs. Many other species of copepods, particularly of the family Choniostomatidae, are parasitic on Crustacea (Hansen, 1897, 1904, 1923).

An extensive and fascinating body of literature on rhizocephalan, epicaridean, and other crustacean parasites and hyperparasites of Crustacea has accumulated (Giard and Bonnier, 1887, 1895; Smith, 1906; Shiino, 1942; Veillet, 1945; Reinhard, 1944, 1956; Baer, 1951; Nicol, 1960).

LOBSTERS

Lobsters, because of their great economic importance in North America and Europe, have been subjects of many scientific studies, including some concerned with diseases and parasites. Because of the practice of holding lobsters in pounds and live cars, occasionally for extended periods and frequently under crowded conditions, mortalities have been observed and causes examined. Two bacterial diseases have significant effects on impounded lobsters. Among the known larger parasites are trematodes, nematodes, acanthocephalans, and annelid worms.

Microbial Diseases

A bacterial disease, caused by gram-positive tetrad-forming encapsulated cocci, described as *Gaffkya homari* Hitchner and Snieszko, is known from wild and impounded populations of American lobsters, *Homarus americanus* Milne-Edwards. The disease (gaffkaemia) was first noted on the Maine coast in 1946 (Hitchner and Snieszko, 1947; Snieszko and Taylor, 1947; Getchell, 1949). "Red-tail" disease, as it was originally called, is characterized by a variable pink coloration of the ventral abdomen, pink blood, prolonged clotting time, and drastic reduction in blood phagocytes. Infected lobsters become progressively weaker, and mortalities may reach 50 percent after short periods of storage. Mortalities increase sharply if water temperature exceeds 15° C. Moribund lobsters move to shoal water and die in a "spread-eagle" position.

Goggins and Hurst (1960)[4] have provided information about two epizootics of gaffkaemia along the entire Maine coast, one in 1946–47 and another in 1959–60, with losses as great as 58 percent of impounded populations. They found that the pathogen could live and multiply outside the lobster, in the slime on lobster cars, crates, tanks, and live wells. *Gaffkya* was also isolated from mud of tidal pounds and from sea water several miles from infected pounds. The disease was transmitted directly by allowing presumably healthy lobsters to feed on infected individuals or by holding healthy lobsters in sea water containing the pathogen. Incubation time was 14 to 21 days, although the animals possibly were already gaffkaemic before the start of the experiments. Treatment of tidal pounds with calcium hypochlorite reduced populations of the pathogen in bottom mud and reduced subsequent losses of impounded lobsters.

The disease organism is often present in wild populations. Stewart and MacDonald (1962) and Stewart, Cornick, Spears, and McLeese (1966) isolated *Gaffkya* from 96 of 2,035 recently caught lobsters in Canada and found the disease to be widespread in the Canadian Atlantic region. Cornick and Stewart (1966) recovered, from presumptive tests for *Gaffkya* in Canadian lobsters, several other kinds of bacteria, including *Micrococcus*, *Pseudomonas*, *Achromobacter*, and *Brevibacterium*—none of which was considered to be pathogenic. Rabin (1965) found a *Gaffkya*-like organism in lobsters from Woods Hole, Mass., and Wood (1965a, 1965b) isolated *Gaffkya*-like organisms from two European lobsters (*Homarus vulgaris* Milne-Edwards) from the North Sea. Wood observed lobster mortalities in storage tanks in southern England in 1962 and recovered *Gaffkya* with cultural and biochemical characteristics similar to Canadian and United States isolates. Epizootics of gaffkaemia have been reported from European lobsters in Ireland (Gibson, 1961), Norway, and the Netherlands (Roskam, 1957). Gibson noted that diseased lobsters were also infested with the "gill maggot," *Nicothoë astaci* Audouin and Milne-Edwards, which was absent from uninfected individuals. Cross sections of the parasitic copepod were used by Gibson to determine the presence of the disease in the host.

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[4] Data provided in unpublished mimeographed report of Department of Sea and Shore Fisheries, Augusta, Maine, "Progress report on lobster gaffkyaremia (Red Tail)," by P. L. Goggins and J. W. Hurst, 1960.

Experimental studies of host-parasite relationships showed that lobsters became infected and died a few days after inoculation with *G. homari* (Rabin, 1965). Prior inoculation with *Vibrio* endotoxin did not enhance the infection and prior inoculation of heat-killed *Gaffkya* did not alter the course of infection. Lobster serum stimulated in vitro growth of *G. homari* in almost every test, but growth of *Vibrio* was sometimes inhibited. Studies of possible defense mechanisms of lobsters against *G. homari* have also been carried out at the Halifax (Nova Scotia) and Saint Andrews (New Brunswick) stations of the Fisheries Research Board of Canada (Fisheries Research Board of Canada, 1966). Lobster serum, as indicated by Rabin's work, had no bactericidal activity against the pathogen but instead promoted its growth.

A preliminary note by Bell and Hoskins (1966) described experimental transmission of *G. homari* to Dungeness crabs and spot shrimps (*Pandalus platyceros*). Infection was achieved by intramuscular inoculation, but not by ingestion or contact. Mortalities were produced in both species.

A second bacterial disease of lobsters, known as "shell disease" (Hess, 1937), is caused by chitin-destroying gram-negative bacilli. Hess isolated chitin-degrading bacteria from live lobsters impounded at Yarmouth, Nova Scotia, but collected from various parts of the Canadian Maritime provinces. This was the first report of attacks by such microorganisms on living Crustacea. The disease was characterized by a pitting and sculpturing of the exoskeleton (fig. 8); although it was first seen in impounded lobsters, similar conditions were later observed in freshly caught lobsters from several widely separated Canadian fishing grounds. Initial lesions occurred on the walking legs, and were distinguished by white outer margins, from which the bacteria were most readily isolated. Hess found the disease relatively rare in natural populations but noted severe shell erosion and weakening of lobsters stored in pounds over the winter. Microorganisms isolated were biochemically and physiologically similar to *Bacillus chitinovorous* Type II and Type XIV of Benton (1935). All isolates were able to decompose pure chitin in saline solution containing no other nitrogen or carbon source. None of Hess' isolates—nor, for that matter, isolates

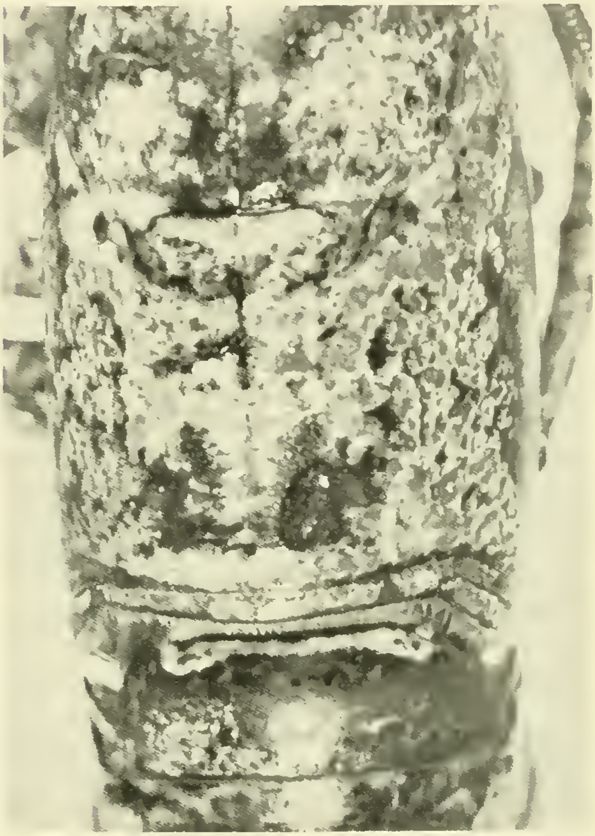

FIGURE 8.—"Shell disease" of American lobster.

prepared in subsequent work—was reported to reproduce the disease experimentally.

Significant mortalities of lobsters accompanied the shell disease; Taylor (1948) found that 71 percent of infected captive lobsters died from the disease, but observed no correlation between mortality and intensity of external shell erosion. Contraction of the disease by healthy lobsters placed in sea-water tanks with infected individuals indicated direct transmission. The disease developed slowly, requiring at least 3 months before the advanced stages were reached. Progress of chitin destruction was directly temperature-dependent, and new shell laid down after molting was not affected, except by reinfection.

Sawyer and Taylor (1949) observed that shell disease produced thickening or complete destruction of the chitinous layer of the gill filaments. No living gill tissue was attacked, but the authors postulated respiratory impairment as an important consequence of the disease. The infection appeared to be entirely external, confined to the exoskeleton, and not invading living tissue nor transmitted internally. Sawyer and Taylor also reported the disease to be present on the Maine coast as well as in Canada, and considered it a potential threat to the lobster industry, in view of the ease of transmission and the observed mortalities of captive individuals. The method of infection of lobsters is unknown; lodging of bacteria in pores and ducts of the shell was proposed by Sawyer and Taylor as a route of invasion.

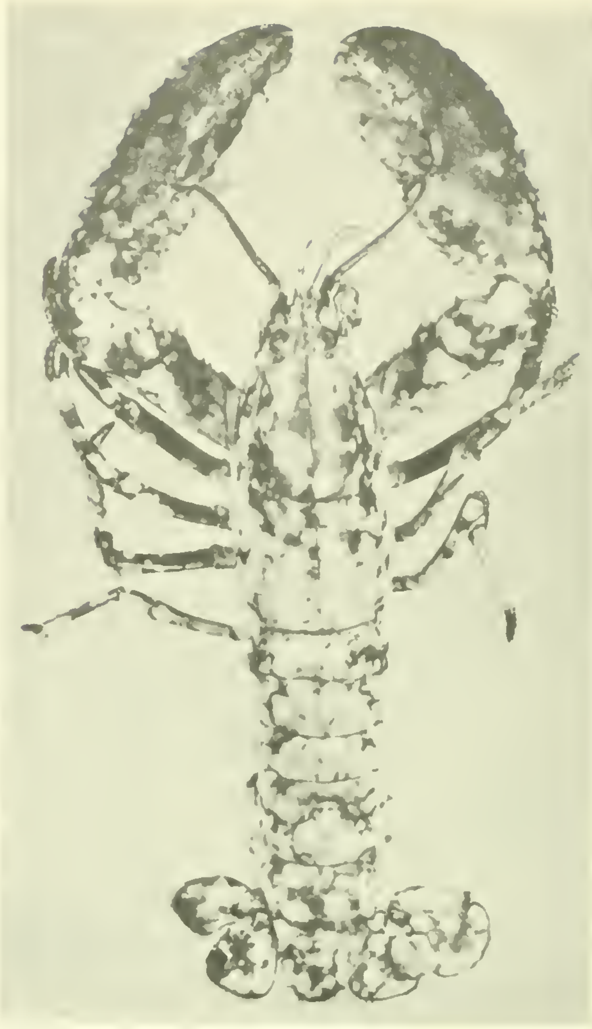
FIGURE 9.—"Leopard lobster" with external signs of mottling disease.

Another recently recognized disease of lobsters from the Maine coast, probably of fungus etiology, is called "mottling disease." Characterized by yellowish splotches in an otherwise dark green exoskeleton (fig. 9), the condition has been known for many years as a color variation. Affected individuals are called "leopard lobsters" (Herrick, 1895, 1911). The shell condition and color result from progressive growth of areas of necrosis in underlying tissues and, in advanced cases, even blisters of the shell. The areas of necrosis expand slowly in lobsters held in sea water tanks. Our histological examination of diseased tissues disclosed numerous Schiff-positive, subspherical, heavy-walled bodies 30 to 60μ in diameter. Tentatively, the organism is considered a chytrid fungus. Preliminary attempts at culture and transmission have been unsuccessful. The disease occurs infrequently in Gulf of Maine lobster populations and has not been reported from other areas.

Dannevig (1928, 1939) in a report on Norwegian lobster hatcheries, described infection and destruction of eggs on the female by the suctorian *Ephelota gemmipara* Hertwig. The protozoan was found on newly caught individuals, and increased tremendously on lobsters in hatching boxes. Dannevig attributed substantial decreases (90 percent) in production of larvae to the effects of the parasite. The organism was abundant only in certain years.

The gregarine protozoan, *Porospora gigantea* (Van Beneden), has been reported as parasitic in the digestive tract of the European lobster (Hatt, 1928, 1931), and was found in all of 202 American lobsters examined from the Magdalen Islands, Gulf of Saint Lawrence, Canada, by Montreuil (1954). *Porospora nephropis* has been described from the Norway lobster, *Nephrops norvegicus* L., by Léger and Duboscq (1915a) and Tuzet and Ormières (1962).

"Spiny lobsters" (family Palinuridae) are of economic importance in many parts of the world, but little is known about their diseases (Sims, 1966). One fatal and apparently infectious disease of *Panulirus argus* (Latreille) from Florida waters was observed by H. W. Sims (written communication, April 8, 1967). Affected individuals became disoriented and their abdomens were "milky"—a condition reminiscent of microsporidan infections of shrimps (Sprague, 1950a) and fresh-water crayfishes (Sprague, 1950b; Sogandares-Bernal, 1962), as was pointed out by Sims. Two fungus parasites, *Ramularia branchialis* and *Didymaria palinuri*, have been described recently from the gills of *Panulirus vulgaris* in Italy by Sordi (1958). *R. branchialis* was also found on the gills of *Homarus vulgaris*.

Diseases Caused by Helminths

Immature aspidobothrid trematodes, *Stichocotyle nephropis* Cunningham, encyst in the stomach and intestinal walls of lobsters—*N. norvegicus* and *H. americanus*—from Europe and North America (Cunningham, 1887; Nickerson, 1894; Herrick, 1895; Odhner, 1910; Montreuil, 1954; MacKenzie, 1963). Montreuil found the parasite in lobsters taken near the mouth of the Bay of Fundy in the Gulf of Maine but not in more than 500 lobsters examined from the Gulf of Saint Lawrence. Adult *S. nephropis* parasitize several species of skates and rays (Odhner, 1898; Linton, 1940).

A larval nematode, tentatively assigned to the genus *Ascarophis* Van Beneden, has been recognized from lobsters taken off northeastern United States (Anonymous [Uzmann], 1966; Uzmann, 1967a). Adults of the genus occur in fishes, particularly gadoids (Uspenskaya, 1953). Larvae occurred commonly in lobsters from Georges Bank and several canyons along the edge of the Continental Shelf south of Cape Cod, Mass., but were absent in lobsters from near the coast. The larvae were encysted in the rectal wall of 25 percent of the offshore lobsters examined by Uzmann, who speculated that larvae from lobsters reach maturity in abundant cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.)) populations of Georges Bank.

A larval acanthocephalan, probably of the genus *Corynosoma*, was identified in American lobsters from the Gulf of Saint Lawrence and elsewhere in the Canadian Maritime Provinces by Montreuil (1954). The worms were usually encysted in the thin wall of the intestine, although some had apparently perforated the gut and encysted in the heart and body muscles. Montreuil believed that accidental gut perforation may provide a route of entry for secondary invaders, and account for appreciable mortality. Feeding experiments with cats and seals suggested that the stage of *Corynosoma* in the lobster is not infective to mammals.

Havinga (1921), in a discussion of artificial lobster rearing in the Netherlands, described the attachment of a small green annelid worm, *Histriobdella homari* Van Beneden, to the eggs and to all parts of the bodies of larval and adult lobsters in Norway. He attributed poor success in production of larvae to effects of the worm. The same parasite had been observed earlier (Sund, 1914, 1915) in massive numbers on eggs of lobsters held in floating boxes at Korshavn, Norway, where it was held responsible for destruction of the brood. Every female lobster was infested with thousands of worms, and they also occurred on larvae. Although *H. homari* had not been reported previously from American lobsters, Uzmann (1967b) has recently found it to be widely distributed on the gills of lobsters in New England coastal waters from Maine to Connecticut, and on those from Georges Bank as well.

Diseases Caused by Parasitic Crustaceans

A blood-sucking parasitic copepod, *Nicothoë astaci* Audouin and Milne-Edwards, has been found on the gills of European lobsters. The parasite was prevalent in Scottish waters (Thomas, 1954; Mason, 1958, 1959) and was seen by Korringa (1957b) in lobsters being held in the Netherlands. Mason found infestations to be occasionally heavy, with a maximum of 1,700 copepods on a single lobster. He concluded that such heavy infestations could harm the host through loss of blood and reduction in gill surface available for gas exchange, but that the usual level of infestation (100 or less per lobster) caused little or no harm to the host

Tumors

One of the earliest observations of neoplasms in invertebrates, according to Scharrer and Lochhead (1950), was made by McIntosh and reported by Prince (1897). A lobster tumor originated in the stomach wall and pushed through the carapace behind the eyes, enlarged, and finally killed the lobster.

SHRIMPS

Many shrimps of the families Penaeidae and Pandalidae are of worldwide commercial significance. Shrimps are the most valuable fishery resource in the United States (Lyles, 1966). Parasites and diseases, which may have adverse effects on shrimp stocks, have been studied, particularly in the Gulf of Mexico. Several diseases caused by Microsporida are known, and larval helminths—trematodes, cestodes, and nematodes—have been reported. Isopods and rhizocephalans have also been observed.

Microbial Diseases

Protozoan parasites have been shown to be of significance to commercial shrimp populations of the Gulf of Mexico. Several microsporidan Protozoa cause a condition known as "cottony" or milky" shrimps. *Nosema nelsoni* was described by Sprague (1950a) from the brown shrimp, *Penaeus azteeus* Ives. Affected body muscles had an opaque white discoloration, and black pigment spots occurred externally. The disease was common in bait shrimps as well as in those processed as food. Infected individuals did not survive well in bait tanks and were also discarded in processing plants, thus representing significant losses to the industry (Woodburn, Eldred, Clark, Hutton, and Ingle, 1957; Hutton, Sogandares-Bernal, and Eldred, 1959). Sprague (1950a) found microsporidan spores in the gonads of the white shrimp, *P. setiferus* (L.), some of which he described as *Thelohania penaei*. Earlier, Viosca (1945) reported that "about 90 percent" of white shrimp in Louisiana waters were infected in 1919 by a protozoan disease (not further identified) which destroyed the reproductive organs. If the disease was caused by *T. penaei*, the microsporidan may play a role in fluctuations of the host species when present at epizootic levels. Iversen and Manning (1959) described still another microsporidan, *Thelohania duorara*, from the musculature of pink shrimp, *P. duorarum* Burkenroad, of the Gulf of Mexico. Infected individuals were relatively rare, however, in landed catches. Brazilian brown shrimp, *P. brasiliensis*, also harbor the same parasite (Iversen and Van Meter, 1964).

Several gregarine Protozoa also occur in shrimps. Sprague (1954) tentatively identified as *Nematopsis penaeus* a gregarine from the digestive tract of brown shrimp from Louisiana. The same parasite was observed by Kruse (1959a, 1959b) and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) in several species of shrimps from Florida. Sprague mentioned the possibility of extensive damage to the intestinal epithelium of individuals heavily infected by *Nematopsis*. Kruse described a second gregarine from the digestive tracts of brown and pink shrimps in Florida, and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) observed the same parasite with high frequency in certain samples of pink shrimp from Florida.

Diseases Caused by Helminths

Shrimps occasionally harbor larval helminths. Metacercariae of the trematode *Opecoeloides fimbriatus* (Linton) were found by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) and Sogandares-Bernal and Hutton (1959) in several Florida species. Larval *Microphallus* sp. have been reported from the body muscles and hepatopancreas of pink shrimp (Hutton, Sogandares-Bernal, and Eldred, 1959; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959).

Several larval cestodes of the order Trypanorhyncha have been found in the digestive gland and other organs of shrimps. Larval *Prochristianella penaei* Kruse were identified from four species of shrimps—brown, pink, white, and humpback (*Trachypeneus constrictus* (Stimpson))—from the Florida coast (Sparks and

Mackin, 1957; Woodburn et al., 1957; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; and Kruse, 1959a, 1959b). Aldrich (1965) found the same cestode larvae in *Penaeus aztecus* and *P. setiferus* from the Texas coast. The adult worm was identified from the Atlantic stingray *Dasyotis sabina* LeSueur. Another trypanorhynch larva, unidentified, was seen by Ward (1962) in great numbers in the abdominal muscles, gills, and pericardium of the white shrimp from the Gulf of Mexico.

Trypanorhynch larvae have been found in commercial shrimps from other parts of the world. Yamaguti (1934) reported larvae, probably *Tetrarhynchus rubromaculatus* Diesing, in *Penaeopsis* sp. from Japan. Heldt (1949) took a larval cestode resembling *Eutetrarhynchus ruficollis* (Eysenhardt) from *Penaeus trisulcatus* Leach from the North African coast.

Larval nematodes of the genus *Contracaecum* were found in Florida shrimps by Woodburn et al. (1957), Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and Kruse (1959b). Margolis and Butler (1954) observed adult nematodes, *C. aduncum*, in a single specimen of northern pink shrimp *Pandalus borealis* Krøyer from British Columbia, Canada.

Diseases Caused by Parasitic Crustaceans

Epicaridean isopods are well-known parasites of Crustacea, and several genera occur on shrimps. Baer (1951), for example, stated that the epicaridean *Hemiarthrus abdominalis* (Krøyer) had been recovered from 20 species of shrimps belonging to the genera *Pandalus* and *Spirontocaris*. Joseph Uzmann (personal communication, Jan. 31, 1967) has found *H. abdominalis* on northern pink shrimp from the Gulf of Maine. The parasite has also been reported on *P. borealis* from Greenland (Horsted and Smidt, 1956) but not from Norway or England (Dahl, 1949; Allen, 1966).

Ricketts and Calvin (1962) described the occurrence of the bopyrid isopod *Argeia pugettensis*, which caused unilateral protuberances of the carapace of the black-tailed shrimp, *Crago nigricauda* (Stimpson), from the Pacific coast of the United States. Infestation was estimated at 3 to 5 percent. Japanese "red prawns," *Penaeopsis akayebi* Rathbun, are frequently (up to 70 percent) infested with another bopyrid *Epipenaeon japonicus* Thielemann. Hiraiwa and Sato (1939) found the gonads of parasitized individuals reduced, or in some males, completely atrophied. Presence of the branchial parasite *Bopyrus squillarum* on the shrimp *Leander serrifer* causes suppression of the ovaries and the breeding characters of the pleopods (Yoshida, 1952).

Several rhizocephalans have been reported as parasites of shrimps. Potts (1912) described *Mycetomorpha vancouverensis* from *Crago communis* Rathbun, and Calman (1898) described *Sylon hippolytes* from the dock shrimp, *Pandalus danae* Stimpson, both from Puget Sound, Wash.

DISEASES AS A POSSIBLE CAUSE OF MASS MORTALITIES

Many physical, chemical, and biological variables contribute directly or indirectly to mortalities of commercially valuable marine invertebrates. Various environmental factors and some of their effects have been discussed by Dexter (1944), Brongersma-Sanders (1957), Coe (1957), Mackin (1961), Dickie and Medcof (1963), Medcof and Bourne (1964), and Merrill and Posgay (1964). It seems clear that the actual cause of death in many mass mortalities is often undetermined, even after exhaustive studies such as those of Orton (1924a, 1924b), who studied oyster mortalities in England in 1920–21, and Roughley (1926), who examined oyster mortalities in Australia in 1924–25.

Disease has often been suspected as a cause of mortalities, but the actual disease agent often has proved to be elusive. Hirsch (1921), Dollfus (1923), and Korringa (1952a) reported major mortalities of sea mussels, probably due to a contagious disease, in the period 1900–19. The mortalities reached a peak in 1914–16. Sick mussels lost their byssal attachment, mantles were retracted, meats were thin, and adductor muscles were weak. Histological and bacteriological examinations were inconclusive. Soon thereafter—1919–23—catastrophic mortalities of European oysters occurred in western Europe. Deaths began in 1919 in Mar Piccolo, near Taranto, Italy (Cerruti, 1941), and quickly spread to England and other European countries. Orton (1924a) suspected, but was unable to demonstrate, a bacterial pathogen. Although no infectious agent was directly associated with the mortalities, disease signs such as mantle retraction, pale digestive gland, muscle degeneration, and pustules on the shell and mantle were seen. Ulcerations and pustules on the body and mantle, and shell pustules containing dead or moribund leucocytes were observed in oysters from England and the Netherlands during periods of mortality (Orton, 1937). These signs often result from disease. The exhaustive studies of Orton were supplemented by those of Eyre (1923, 1924), who isolated a number of species of bacteria from sick and healthy oysters, but doubted that any were true pathogens.

Korringa (1952a) gave an excellent historical account of these mortalities of oysters in Europe. Cultured-oyster beds in France, England, Denmark, Germany, and the Netherlands were affected almost simultaneously. Many natural beds were also destroyed. A few isolated populations—Helgoland and Brittany—were not affected until several years later. Mortalities did not occur in Portuguese oysters during this time. Although environmental factors such as poor food supply and low temperatures were held by some to be causes of the catastrophic mortalities (Gaarder and Alvsaker, 1941; Spärck, 1950), the available evidence strongly indicates an infectious disease (Cole, 1951b; Fischer, 1951; Korringa, 1952a).

A mortality, with characteristics very similar to those seen in the European oyster, was described by Roughley (1926) in populations of rock oysters, *Crassostrea commercialis* (Iredale and Roughly), from Australia. Oysters died in 1924 and 1925 in Georges River, New South Wales. Disease signs, such as abscesses and ulcerations, were observed, and a bacterial pathogen was suspected—possibly combined with winter environmental stresses.

Disease-associated mortalities, with a history of long and frustrating scientific study, were first observed in 1915 in American oysters of Prince Edward Island, Canada (Needler and Logie, 1947). In the period 1915–33, the disease (commonly known as "malpeque disease") spread around the Island and destroyed most of the oyster stocks—some of which required 20 years to return to previous levels of abundance (Logie, 1956). During the outbreak, oysters apparently developed resistance to the causative organism, whose identity remains undetermined. Beginning in 1955, mortalities, probably due to the same disease, began in waters of the adjacent mainland of New Brunswick across Northumberland Strait. Oyster populations along the entire northern coast of New Brunswick and Nova Scotia were decimated, but mass transfer of disease-resistant oysters from Prince Edward Island waters, beginning in 1957, has hastened the recovery of the fishery (Logie, Drinnan, and Henderson, 1960; Drinnan and England, 1965).

Pacific oysters imported as seed from Japan and planted in waters of the States of Washington and California began to die in significant numbers in the late 1950's. Oysters in their second year after introduction were most commonly killed; peaks of mortalities occurred in late summer; and deaths were most often observed at the heads of bays. In the absence of other obvious environmental changes, and because of the selective nature of the mortalities, it seems logical to suspect disease. A pathological condition described by us as "focal necrosis," has been found in seed from Japan and in several samples of larger oysters from beds in Washington. As many as 30 percent of the individuals in a sample were affected. In addition, a haplosporidan parasite, morphologically similar to the pathogen *Minchinia nelsoni* associated with recent mortalities on the U.S. east coast, has been seen by staff members of the BCF Biological Laboratory, Oxford, Md., in Pacific oysters from the State of Washington; a similar organism was recognized recently in a sample of seed oysters from Taiwan. Pereyra (1964) mentioned a "multinucleated MSX-like organism, possibly pathogenic" in a dying oyster from Oyster Bay, Wash. No clear association has yet been made, however, of specific pathogens with mortalities of *C. gigas* on the Pacific coast of the United States, and it is quite possible that other environmental factors are operative in the mortality areas.

The Japanese literature contains numerous historical accounts of mass mortalities of oysters dating back to 1915. Although disease was often suspected, specific pathogens were usually not identified. Takeuchi et al. (1960) mentioned large-scale deaths of oysters in Kanasawa Bay, beginning in 1915 and continuing for a number of years. Over 80 percent of the oysters in that bay died annually. Ogasawara et al. (1962) reported similar mass mortalities on the Miura peninsula, beginning in 1927 and continuing for 10 years. Oyster farms along the coast of the peninsula lost 50 to 80 percent of their crop annually. More recent mortalities of 2-year-old oysters have occurred in Hiroshima Bay and adjacent localities, beginning in 1945 (Fujita et al., 1953). A 10-year study (Takeuchi, Matsubara, Hirokawa, and Tsukiyama, 1955, 1956; Takeuchi, Matsubara, Hirokawa, and Matsuo, 1957; and Takeuchi et al., 1960) provided somewhat inconclusive evidence that a bacterial pathogen was responsible for the mortalities.

A series of papers by Tohoku Regional Fisheries Research Laboratory (Imai et al., 1965; Kan-no et al., 1965; Mori, Imai, Toyoshima, and Usuki, 1965; Mori, Tamate, Imai, and Itikawa, 1965; Numachi et al., 1965; Tamate et al., 1965) described mass mortalities of oysters in Matsushima Bay, Miyagi Prefecture, Japan, that have occurred annually in late summer since 1961. Environmental, physiological, and pathological factors were examined. Pathological changes were observed, and mortalities were considered to be related to metabolic changes during fattening and spawning. Mortalities exceeded 60 per cent per year in certain areas of the Bay during 1961–64. A gram-positive bacterium was found in multiple abscesses in as many as 20 percent of oysters in certain samples (Numachi et al., 1965), but a causal relation with mortalities was not established. Our later studies suggest that the disease condition is the same as that called "focal necrosis" in adult Pacific oysters from Washington. The pathogen warrants further observation, since the abscesses may represent only the chronic stage of infection in resistant hosts, whereas the acute disease may have a significant effect on mortality. An ameboid organism, often present in large numbers and accompanied by pronounced host response, has also been found in oysters from the Matsushima Bay mortality area.

Blue crab populations on the coasts of North and South Carolina have been affected by extensive mortalities beginning in 1965 (Lunz, 1967). Significant impact on population size was indicated by a marked drop in catch per unit effort in 1966, as compared with the previous 5 years. Newspapers stated that great numbers of crabs were washed up on beaches or littered the bottoms of creeks, and that catches were drastically reduced. Disease has been suspected (Lunz, 1967), but no clear evidence of a pathogen has been obtained. Such mortalities in wild crabs are apparently distinct from the long-recognized high levels of deaths in crab shedding floats (Beaven and Truitt, 1939), which may in part be associated with parasites or diseases (Couch, 1966; Sprague and Beckett, 1966).

A few mass mortalities of marine invertebrates have been definitely ascribed to epizooties caused by specific pathogens (Sindermann, 1963). Recurring mortalities of American oysters in the Gulf of Mexico were found to be caused by the fungus *Dermocystidium marinum*. Exerting its effects in higher salinities and temperatures among dense aggregations of hosts, the pathogen can cause annual mortalities in excess of 50 percent. Development and use of a presumptive test, with thioglycollate medium (Ray, 1952), has established the presence of the organism in oysters throughout the Gulf of Mexico and northward along the Atlantic coast as far as Connecticut. Although the fungus may at times reach epizootic levels in particular areas, its most significant effect is probably that of continuing attrition, year after year, during periods of high sea-water temperature. Effects of the disease on commercial beds are now controlled to some extent by planting and harvesting at prescribed times of the year and by spreading oysters thinly on the beds.

Major mortalities, with consequent severe depression of the oyster fishery, occurred in Delaware and Chesapeake Bays on the U.S. east coast, beginning in the late 1950's. A haplosporidan parasite with distinctive characteristics, *Minchinia nelsoni*, has been associated with the mortalities. Epizootic areas have had oyster losses in excess of 90 percent, and some indications are appearing of increased resistance among survivors. The disease, like that caused by *Dermocystidium*, exists and exerts severe effects in salinities above 15 o oo. Seed beds and oyster stocks in low-salinity areas have not been destroyed. Recently the organism has been found in oyster populations on the coasts of New York and North Carolina—well outside previous areas of high mortality.

Studies of these serious pathogens of oysters —*D. marinum and M. nelsoni*—have revealed the very important role of a "salinity barrier" to certain diseases. The fungus *D. marinum* exerts severe effects on oyster populations in high-salinity waters of the Gulf of Mexico but does not flourish in low-salinity areas. *M. nelsoni*, which has seriously affected oyster stocks of the Middle Atlantic States, also occurs in higher salinities. Both pathogens seem confined to salinities above 15 o oo; this fact has made possible the continuation of production in parts of coastal areas affected by these epizootics.

Inhibitory effects of low temperature have been well illustrated for these serious oyster pathogens. *D. marinum* causes warm-weather mortalities in American oysters; in fact, the plantings of seed oysters are timed to take advantage of the relative quiescence of the disease in cooler seasons. Surveys of *Dermocystidium* have indicated marked decline in winter. *M. nelsoni*, of Chesapeake Bay and Delaware Bay, is similarly quiescent in winter. New infections are not apparent, prevalence of disease declines, existing infections seem less active, and mortalities are reduced.

Mackin (1961) attempted, from a review of the literature, to itemize characteristics of mortalities of oysters due to various causes. As one who has published extensively on the role of disease in oyster populations, he naturally turned his attention toward mortalities caused by infectious agents. Among many interesting comments in his paper, Mackin stated that "all oyster producing bays are endemic areas for one or more diseases" and that "not only are bivalve mollusks frequent hosts for pathogens, but they are regularly parasitized by a unique group of low fungi." Mackin further stated his belief that "of all causes of mortality, disease ranks first." Disease, then, can cause significant, if temporary, reductions in population abundance of marine invertebrates. Such reductions may exceed 95 percent of existing stocks. Additionally, there is every indication that serious but undescribed diseases exist among marine invertebrates. Mackin (1962), for example, mentioned a number of pathological conditions in oysters that were not associated with known pathogens. Rust disease of Pacific king crabs, which we have described on the basis of an unpublished report, is a commonly recognized condition in the fishery, but has not been described in the published scientific literature.

Destruction of most of a population by epizootics and mass mortalities, of course, also reduces pathogen numbers, because the possibility of finding a new susceptible host at a critical point in the life cycle is reduced.

Less spectacular mortalities, which also have severe continuing depressive effects on host population size, are probably more common than large-scale or mass mortalities. Minor fluctuations in abundance may be attributable to such "background" mortalities. Also, those parasites and diseases that do not kill the host may act as indirect agents of mortality. Abnormal individuals are rendered more vulnerable to predation in many ways: their body muscles may be partially destroyed, covering or erosion of their gills may interfere with respiration, or their normal protective coloration may be modified or obscured. For example, Hopkins (1957a) has observed that blue crabs prey more frequently on oysters which cannot close their shells as quickly or as tightly as normal oysters. Any increase in parasite burden must reduce the probability of survival in an environment where death, early and sudden, is the rule rather than the exception. For parasites with complex life cycles involving two or more hosts, consumption of an earlier host in the cycle—one weakened by the parasite—by the right predator may be critical to the completion of the cycle.

Another prominent effect of parasitization of marine mollusks and crustaceans is sterilization of the host. Larval trematodes are notable for destroying the gonads of gastropods and bivalves, and parasitic barnacles and certain isopods produce similar effects in crustaceans. In areas where levels of parasitization are high, the reproductive capacity of the host population may be seriously impaired. In a study of the ecological relation of the marine snail, *Littorina littorea*, and its trematode parasite, *Cryptocotyle lingua*, Sindermann and Farrin

(1962), and Sindermann (1965, 1966a) found prevalences of the parasite of over 50 percent in certain coastal areas, indicating that the reproductive potential of snail populations was suppressed by that amount. An excellent review of parasitic castration of Crustacea has been provided by Reinhard (1956).

Effects of disease can be generally categorized as catastrophic, resulting in mass mortalities, or continuing, producing a constant drain on population numbers. Although disease is always with us, and mortalities have undoubtedly occurred in the past, new factors have been introduced by man to set the stage for the spread of epizootic disease. For example, oysters are transferred promiscuously from one geographic area to another; populations are often crowded in dense beds, sometimes in areas where natural populations did not exist previously; drastic physical and chemical changes have been made in oyster habitats; and new predators have been introduced. A dominant mortality factor—disease—has been aided by human activities; it must be controlled, if we are to achieve maximum production of cultivated inshore mollusks and crustaceans.

Many different environmental factors—physical, chemical, and biological—can kill oysters, crabs, or other animals of commercial value (Brongersma-Sanders, 1957). Any single factor may become overriding, however, at a particular time in the life of a species—and in this paper we have described several examples of how the factor of disease can reduce the abundance of marine species.

It is easy, of course, to overextend any point of view; we do not imply here that every decrease in abundance can be blamed on disease. An excellent case could also be made from the published literature for the significant role of predation—particularly during population peaks of particular predator species—as a major cause of fluctuations in abundance of commercially valuable species. Man-made changes in environment can also affect abundance. Because of industrial pollution, shellfish populations have been eliminated from certain localized areas within estuaries and along the coast. In addition, other types of pollution have made extensive areas in rivers and bays unavailable for the harvesting of shellfish. It is likely that mass mortalities are, and have always been, natural methods of population regulation—but, until recently, these mortalities would have been accepted with the same dazed bewilderment and inaction that must have characterized the behavior of our ancestors during the plagues of the dark ages. We can now look to methods of environmental control and stock manipulation, particularly for sedentary shallow water species such as oysters, clams, and even certain Crustacea, as part of the methodology of an increasingly complex system of cultivation of our inshore waters.

CONTROL OF DISEASES OF MARINE INVERTEBRATES

The original, persistent, and largely erroneous feeling about disease in marine populations is that little can be done about it. This pessimistic attitude is definitely unwarranted for species that live inshore—particularly the sedentary invertebrates—where practical measures of disease control are possible and have already been applied in some situations. Possible methods include the following:

1. *The transfer of susceptible animals into epizootic areas, or of individuals from such areas, should be prevented.* Because each disease is discrete in terms of transmission and infectivity, risks of transfer will vary as well. When intermediate or alternate hosts play a significant role in maintaining the disease in a given geographic area, transfer of infected individuals to other areas where these hosts are absent may be a reasonable management procedure. Diseases that have been demonstrated experimentally to be transmitted directly, however, such as *Dermocystidium* infections of oysters, may be maintained at epizootic levels by repeated introduction of susceptible animals.

2. *Disease-resistant stocks should be developed by selective breeding of survivors.* Epizootics of several oyster diseases have apparently produced increased resistance among survivors. During the outbreak of "malpeque disease" in Prince Edward Island (Canada) oysters, resistance developed to an unidentified pathogen, and stocks returned to previous levels of abundance after several decades. That the pathogen is still present is indicated by deaths of suscep-

tible oysters from other geographic areas introduced into Prince Edward Island waters. Resistant stocks were drawn upon to repopulate other oyster growing areas of the Gulf of Saint Lawrence that had been subsequently decimated by the same disease.

Evidence is accumulating that increased resistance to the haplosporidan pathogen *Minchinia nelsoni* is developing among oysters that have survived the disease in the Middle Atlantic States. The disease has been at epizootic levels in some Chesapeake Bay populations for several years. Perhaps resistant strains can be developed with presently available hatchery techniques. Aggregation of survivors on natural beds to which adequate cultch has been added could also do much to improve reproduction, spatfall, and return to full production.

3. *Basic information about the life history and ecology of the disease agent must be accumulated, to define vulnerable stages or restrictive environmental requirements.* As an example, several oyster pathogens, such as *M. nelsoni*, are limited to salinities in excess of 15 o oo. Plantings during epizootics can be restricted to low-salinity areas, and temporary transfer of infected stocks to low salinities may retard or eliminate infections. Mechanical and chemical treatments can also reduce disease prevalence. Effects of gaffkaemia on impounded lobster populations have been reduced by treating bottom muds of pounds with calcium hypochlorite. Damages of dermocystidium disease to oysters have been lessened by planting oysters thinly on the beds, by harvesting within 2 years, and by planting and harvesting at prescribed seasons to take advantage of the decrease in pathogen activity during the colder months.

Korringa (1959) outlined an extensive program to control the spread of the parasitic copepod *Mytilicola* in cultivated mussel stocks of the Netherlands. Included were extensive dredging of adjacent natural beds, transfer of lightly infested stocks, and destruction of heavily infested beds.

Korringa (1951a) found "shell disease" of oysters to be caused by a fungus that perforated the shell—a fungus that thrived on old shells. He attributed the outbreak of shell disease in 1930 in the Netherlands to the practice of spreading enormous quantities of cockle shells on the beds. The disease declined when the spat collectors were placed in areas free of the disease, when old shells were cleared from beds, and when infected young oysters were dipped in mercuric disinfectant (Korringa, 1948, 1949, 1951c).

Biological control of other hosts in the life cycle of parasites, or biological control of the parasite itself, are also possible approaches.

4. *Production could be maintained in artificial environments where disease can be controlled.* Some progress has been made in this direction with the development of hatchery methods of producing seed oysters and clams (Loosanoff and Davis, 1963). Bacterial and fungal epizootics in larval culture tanks can be prevented, or their effects reduced, by ultraviolet treatment of filtered sea water, antibiotic treatment of sea water in standing water cultures, maintenance of general cleanliness of all utensils used in handling larvae, and ultraviolet treatment of phytoplankton food derived from impure mass cultures.

Shellfish production in artificial ponds (Shaw, 1965) offers distinct possibilities of disease and predator control, beginning with disease-free and disease-resistant brood stock and progressing to filtration and ultraviolet treatment of recirculated water; important also are careful control of contaminants in mass phytoplankton cultures and elimination of shellfish associates that act as alternate or intermediate hosts of disease agents.

CONCLUSIONS

Many of the great fisheries of the world have undergone large fluctuations in supply. The causes of these fluctuations, although subjects of much discussion, have rarely been precisely determined. Reduction in abundance of commercially valuable marine species has been attributed to overfishing, failure of spawning, sudden and drastic changes in temperature and salinity, and many other factors. One biological factor that has received too little attention is disease. The fact that marine animals become ill and die, often in vast numbers, has been largely ignored. Events in commercial shellfish populations in this century, however, have forced us to look closely at disease as a cause of mass mortalities of epic proportions, and of subsequent major declines in abundance of commercial species.

Molluscan and crustacean species of economic value as food have been affected by diseases, some of which have produced epizootics with resultant mass mortalities. Much attention has been directed toward oyster diseases, possibly because oysters have been cultivated more intensively than most other inshore or estuarine species. Microbial diseases—including those of bacterial, fungal, and protozoal etiology—have affected oyster stocks in many parts of the world. Bacterial diseases have had serious effects on lobsters, and a number of Protozoa, particularly Microsporida, affect crab and shrimp populations.

It is often difficult to establish the precise cause of death of marine invertebrates—to determine whether a suspected pathogen is a primary or secondary invader. Environmental and physiological factors can be inextricably associated with apparent disease; their relative effects are often not easy to assess. Thus, the literature on mass mortalities contains measurements of many environmental variables, descriptions of physiological conditions of host animals, and reports of suspected disease agents—but too frequently the studies have been unable to point to a single cause of death. The search for a single cause may have been an oversimplified approach to a complex problem. In other situations, epizootics of specific pathogens, possibly influenced to some extent by environmental factors, can be directly related to the state of resistance of the host population, the virulence and infectivity of the pathogen, and infection pressure.

Mass mortalities, many of undetermined causes but some definitely the result of disease, have occurred in commercial invertebrate populations. These mortalities are a natural method of regulating population size; they have received increasing scrutiny in recent years. The development of methods of cultivation and of limited manipulation of the inshore environment should make it possible to reduce or eliminate the serious threat of disease to populations of commercial shellfish.

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SOME FEATURES OF THE GULF STREAM OFF CHESAPEAKE BAY IN THE SPRING OF 1963[1]

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ABSTRACT

Oceanographic measurements in May and June 1963, showed that water mixing was intense though intermittent at the western boundary of the Gulf Stream. Warm, saline water became separated from the Stream and mixed with the slope water as a result of divergence near the surface and upwelling. Data from repeated sections along three transects of the Gulf Stream are analyzed and presented in 22 cross-sectional plots. These plots show that a zone of intense mixing appeared intermittently at the western side of the Gulf Stream in an apparently fluctuating manner. Separation of this mixing zone from the Gulf Stream resulted from local ascent of cool water from the subsurface levels where there was a zone of steeply sloping isotherms. The results suggest that part of the mixed, dense water sank to about 200 m. below the depth at which it was produced and returned to the Gulf Stream.

Data for this report were obtained during Cruise 1 of the Bureau of Commercial Fisheries research ship *Geronimo* (May 8 to June 7, 1963). Although the primary purpose of the cruise was to test the ship and its gear, extensive physical and biological oceanographic observations were also made. The principal physical investigation was a study of the properties of the Gulf Stream along three transects described as follows (fig. 1):

Transect I—16 sections across the left (inshore or western) boundary of the Gulf Stream—12 with bathythermograph observations only, and 4 with oceanographic stations (Nansen bottle casts) and BT's.

Transect II—four sections across the left boundary (all with oceanographic stations and BT's).

Transect III—three sections across the left boundary (all with oceanographic stations and BT's).

Most of the data used in this report were gathered by repeated occupation of these transects. For each transect, one section was extended southeastward into the Sargasso Sea. The right (offshore or eastern) boundary of the Gulf Stream was crossed six times.

Bathythermograph observations were taken every 5 nautical miles (9.3 km.), except that on a supplementary run from transect II to transect I along the left boundary, BT's were taken every 10 miles (18.5 km.). Observations at the oceanographic stations were limited to the upper 600 m. The last one or two digits in the numbers of the hydrographic station locations used in this report (fig. 1) indicate their chronology.

Continuous records of surface temperature were made with a Foxboro [3] thermograph and were checked by measurements with two thermistors and one bucket thermometer at the location of each BT observation. Portions of the Foxboro temperature records are reproduced (figs. 2 and 3 to 25). The lower trace on the temperature record is used when the upper trace exceeds the scale and is usually set 10° C. below the upper. The lower trace was not well controlled during this study, and the difference at times exceeds 10° C.

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[1] Contribution No. 53, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Fla. 33149.

[2] Now at U.S. Naval Oceanographic Office, Code 7240, Naval Research Laboratory, Washington, D.C. 20390.

[3] Trade names referred to here do not imply endorsement of commercial products.

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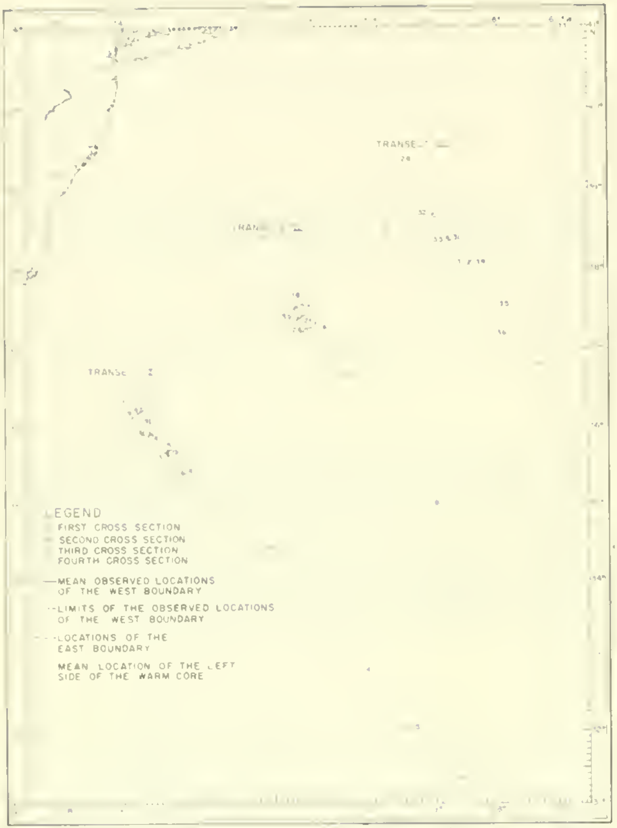

TRANSECT
TRANSECT
TRANSECT
LEGEND
FIRST CROSS SECTION
SECOND CROSS SECTION
THIRD CROSS SECTION
FOURTH CROSS SECTION
MEAN OBSERVED LOCATIONS OF THE WEST BOUNDARY
LIMITS OF THE OBSERVED LOCATIONS OF THE WEST BOUNDARY
LOCATIONS OF THE EAST BOUNDARY
MEAN LOCATION OF THE LEFT SIDE OF THE WARM CORE

FIGURE 1.—Locations of transects and (oceanographic) stations of R.V. *Geronimo* Cruise 1.

Continuous representation of the Gulf Stream structure along its axis is not possible because the observations were concentrated on transect lines about 140 miles (259.4 km.) apart. The detailed observations along each line do reveal a number of common properties among the transects. Most sections extend across only the left boundary of the Gulf Stream; therefore, my main intent is to interpret some variable and transient features of that boundary.

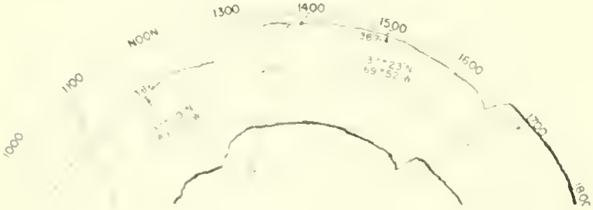


FIGURE 2.—Thermograph record of surface temperature change across the right boundary of the Gulf Stream between transects II and III. Temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers and locations are indicated along the temperature trace.

BOUNDARY SYSTEM

In defining the boundary system, I will describe the temperature structure in the area between the slope water and the Sargasso Sea.

SLOPE WATER—INTERMEDIATE WATER BOUNDARY

From the slope water to the Gulf Stream, the surface temperature increased in two steps along most of the sections. In a typical case (fig. 10), the first step was a positive gradient of about 8° C. in less than 1 mile (1.9 km.); this temperature increase was the offshore (eastern) boundary of the slope water. Beyond this first step was a rather wide intermediate area of very irregular surface temperatures. Another steep, positive surface gradient of about 4° to 6° C. was at the left boundary of the Gulf Stream; in most sections this gradient was above or slightly left of the zone of steeply sloping isotherms in the subsurface layers. Iselin (1936) reported similar observations of the slope water and Gulf Stream boundaries.

INTERMEDIATE ZONE

The width of the intermediate zone—between the offshore slope water and the inshore Gulf Stream boundaries—varied greatly. At times it was not observed at all; at other times it was as wide as 60 miles (111.1 km.). For example, the zone is practically nonexistent in figure 5, where surface temperature increased from 12° to 22° C. in about 3 miles (5.6 km.), followed by an increase of only about 2° more in the next 20 miles (37 km.) (the distance to the warm core). A contrasting situation is illustrated in figure 18, in which the intermediate zone is about 50 miles (92.6 km.) wide and the warm core of the Gulf Stream is immediately to the right of the Gulf Stream boundary.

LEFT BOUNDARY OF THE GULF STREAM

The left boundary of the Gulf Stream is defined here as the first strong thermal gradient crossing at the surface from the Gulf Stream toward the slope water. The mean location of

DATE	10-MAY-63	—	—	—	—	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—	—	—	—	—
NO. OF BT	2	3	4	5	6	7	8	10	12
G.M. TIME	1240	1300	1330	1400	1430	1500	1530	1730	1835
LATITUDE (NORTH)	36°31'	36°27'	36°25'	36°22'	36°20'	36°17'	36°13'	36°09'	36°06
LONGITUDE (WEST)	74°06'	74°02'	73°58'	73°55'	73°51'	73°46'	73°43'	73°33'	73°29'
SURFACE SALINITY ‰	—	—	—	—	—	—	—	—	—
SURFACE TEMPERATURE °C.	12.1	12.4	11.6	17.7	18.7	16.4	21.8	21.2	25.2

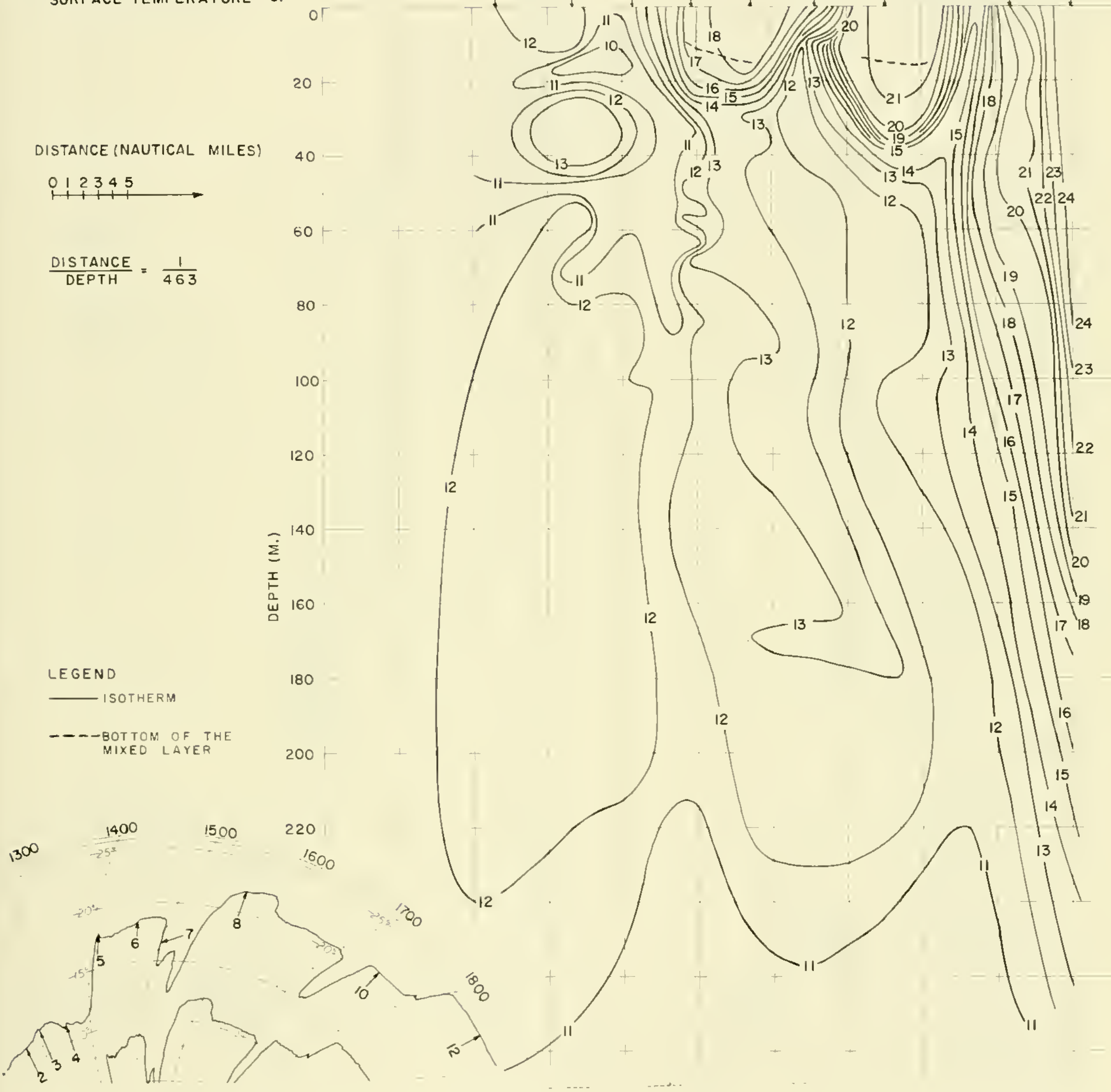


FIGURE 3.—Transect 1—Section 1, May 10, 1963. Vertical temperature profile and thermograph record of surface temperatures. Thermograph temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers appear along the surface temperature trace to show the time of the casts.

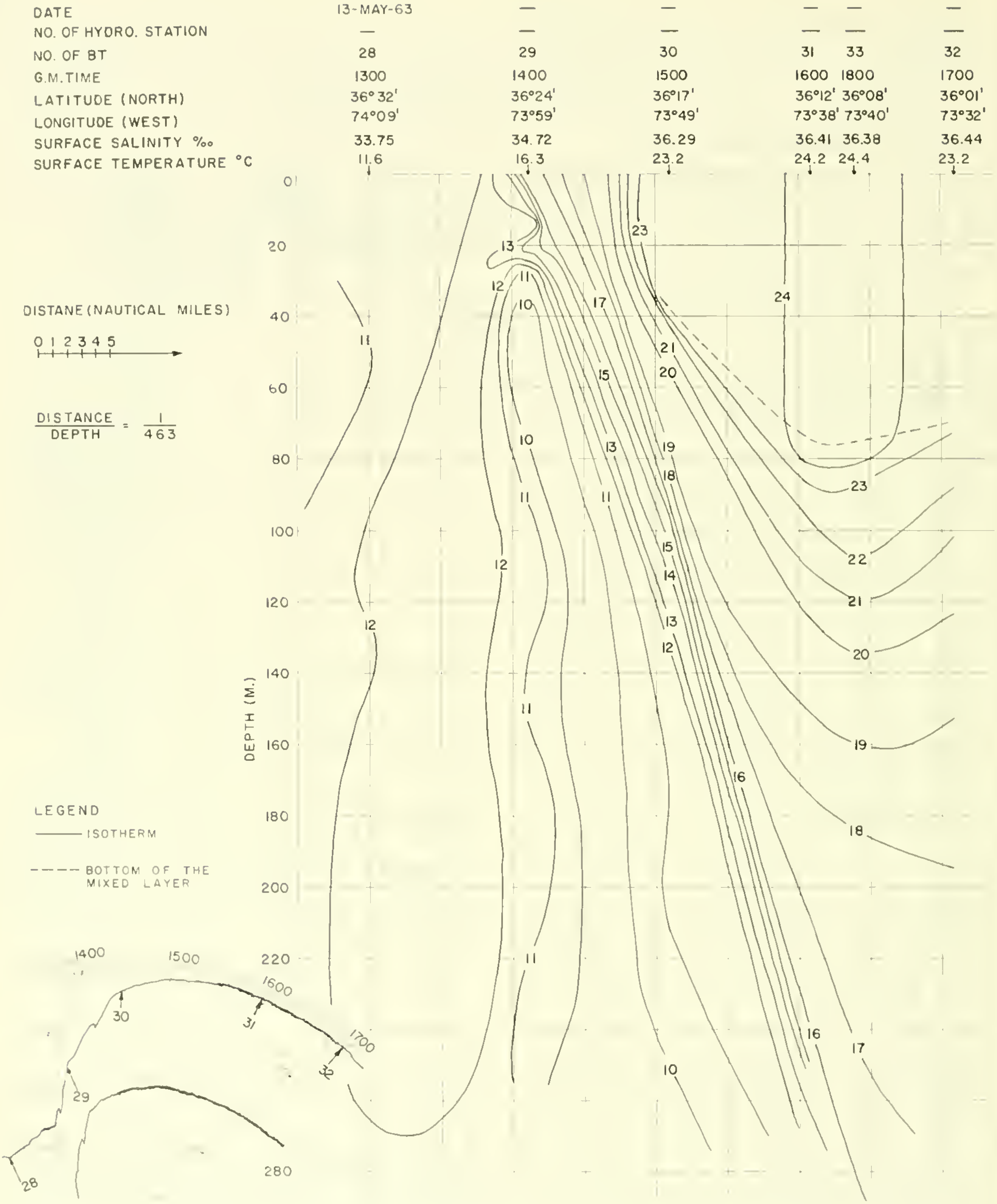


FIGURE 4.—Transect I—Section 2, May 13, 1963. (*See* caption for fig. 3.)

DATE	13-MAY-63	—	—	—
NO. OF HYDRO. STATION	—	—	—	—
NO. OF BT	36	35	34	33
G.M.TIME	2100	2000	1900	1800
LATITUDE (NORTH)	36°30'	36°21'	36°15'	36°08
LONGITUDE (WEST)	74°06'	73°51	73°48	73°40'
SURFACE SALINITY ‰	33.87	36.29	36.38	36.28
SURFACE TEMPERATURE °C.	11.8	23.3	23.6	24.4

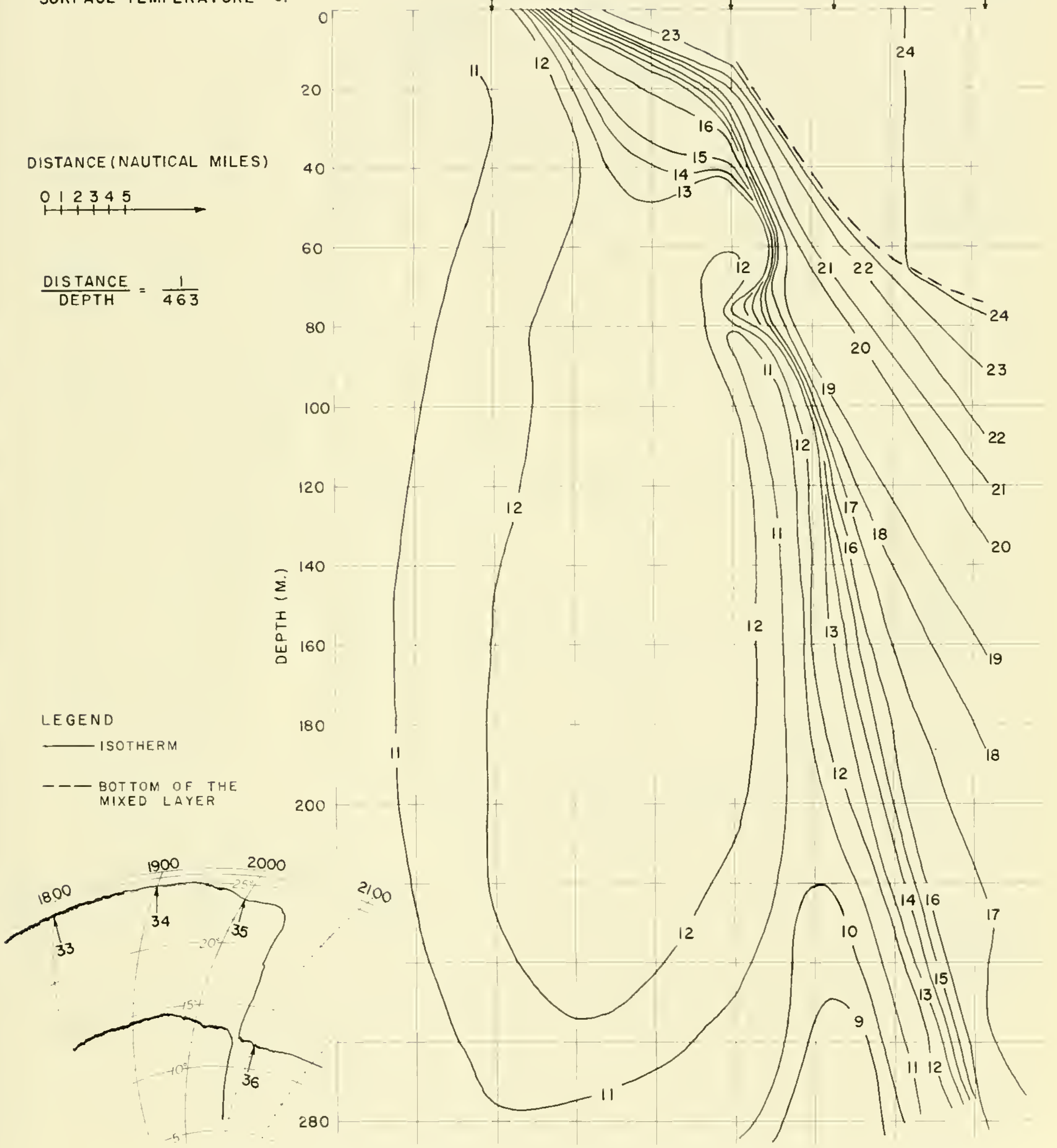


FIGURE 5.—Transect I—Section 3, May 13, 1963. (*See* caption for fig. 3.)

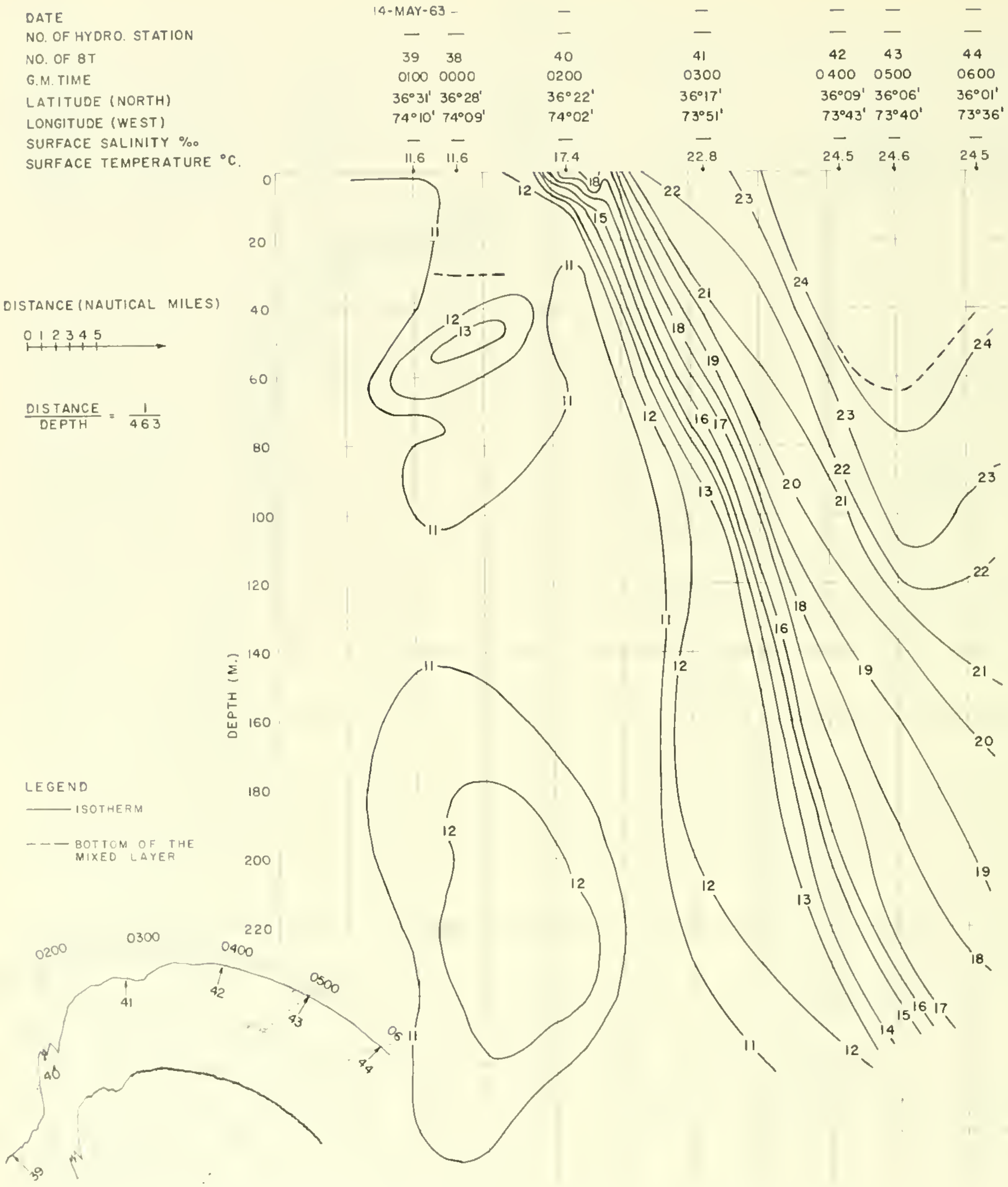


Figure 6.—Transect I—Section 4, May 14, 1963. (*See* caption for fig. 3.)

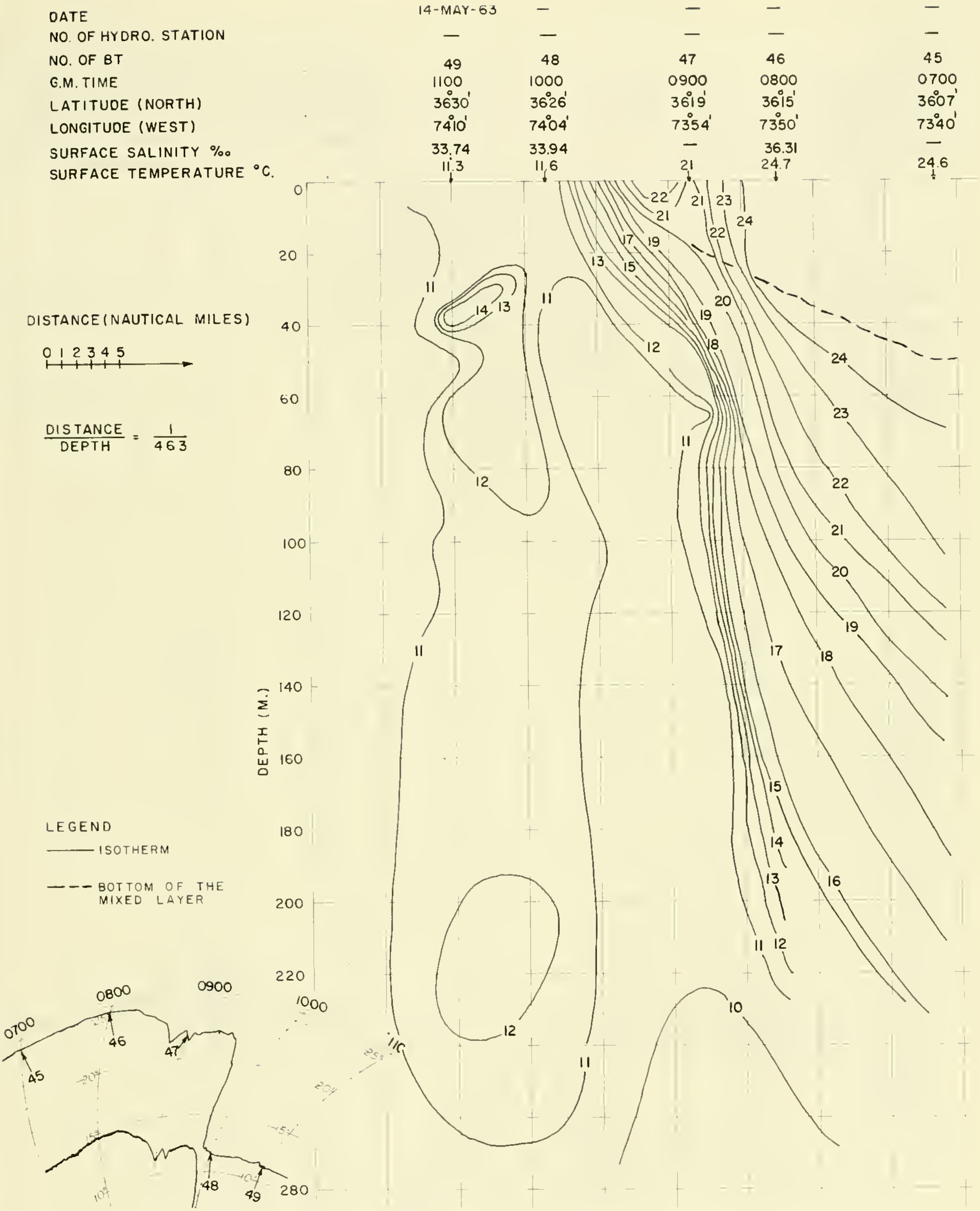


FIGURE 7.—Transect I—Section 5, May 14, 1963. (*See* caption for fig. 3.)

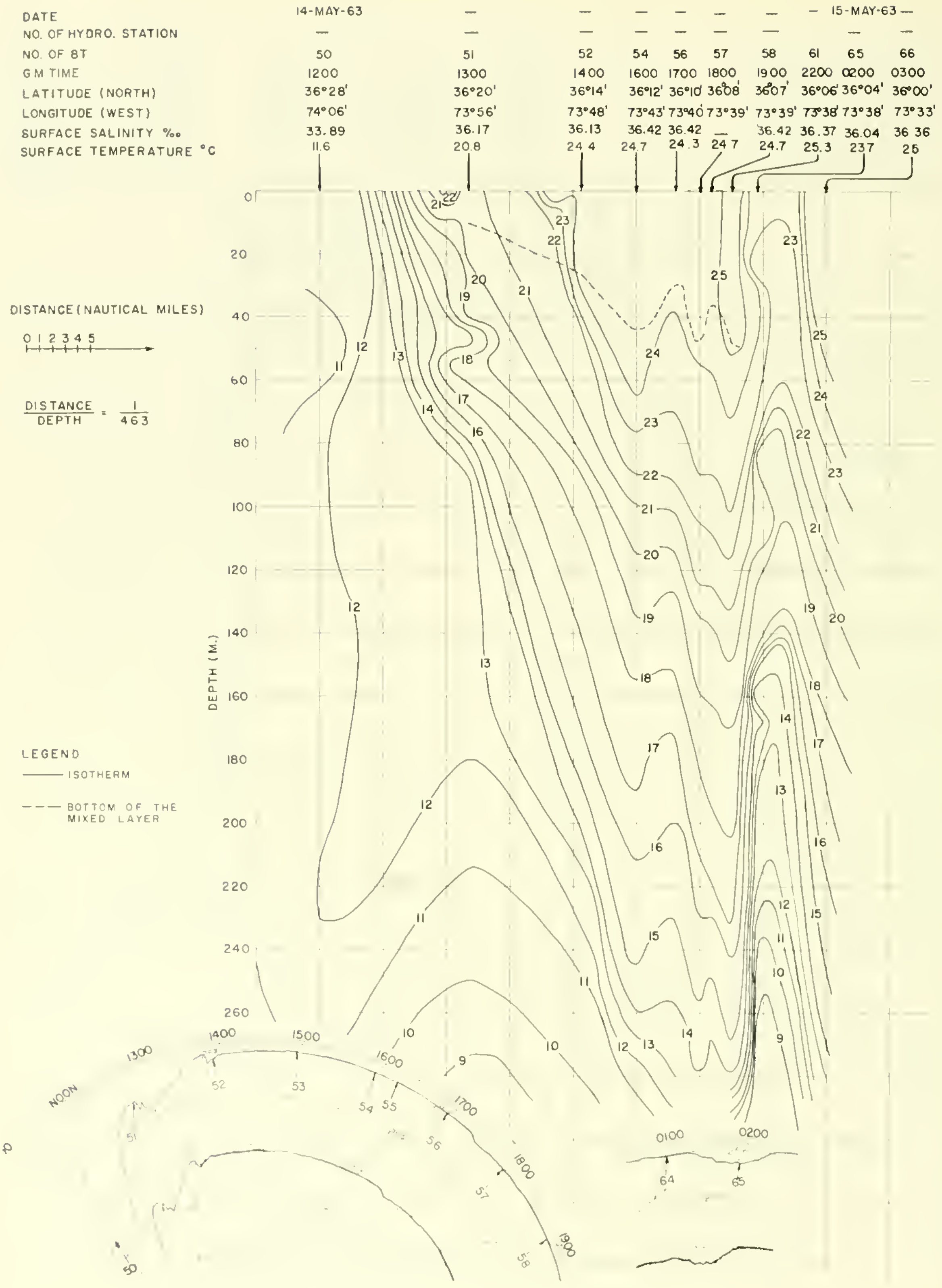


FIGURE 8.—Transect I—Section 6, May 14, 1963. (*See* caption for fig. 3.)

DATE	15-MAY-63	—	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—	—
NO. OF BT	71	70	69	68	67	66
G.M.TIME	0800	0700	0600	0500	0400	0300
LATITUDE (NORTH)	36°31'	36°26'	36°17'	36°12'	36°03'	36°00'
LONGITUDE (WEST)	74°08'	74°01'	73°55'	73°47'	73°35'	73°33'
SURFACE SALINITY ‰	33.90	34 52	35.57	34 86	—	36.36
SURFACE TEMPERATURE °C.	12	12.4	19.8	18.4	20.2	25

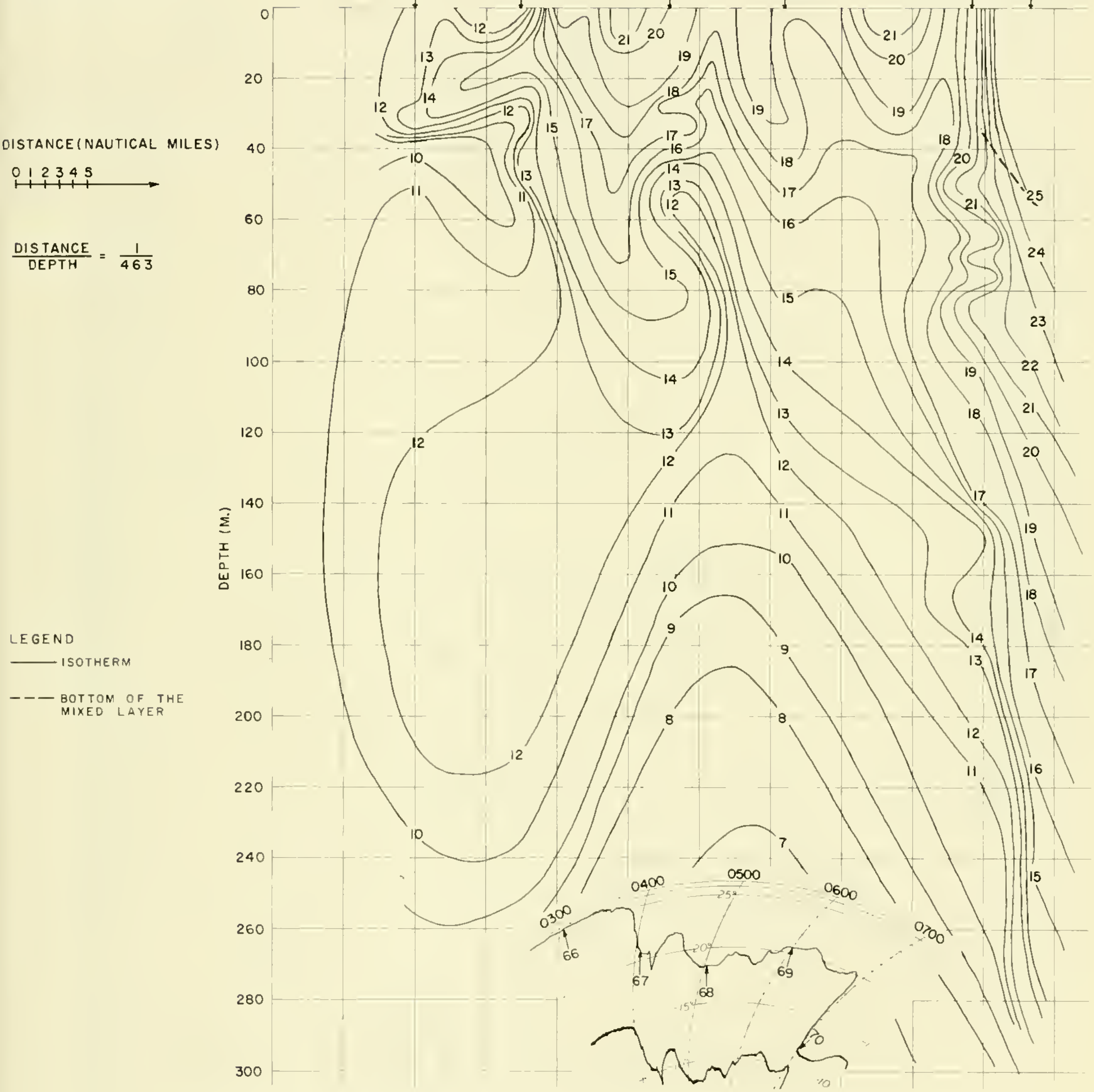


FIGURE 9.—Transect I—Section 7, May 15, 1963. (*See* caption for fig. 3.)

DATE	15-MAY-63	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—
NO. OF BT	72	73	74	75	77
G.M.TIME	0900	1000	1100	1200	1355
LATITUDE (NORTH)	36°25'	36°17'	36°09	36°03'	35°59'
LONGITUDE (WEST)	74°01'	73°54'	73°45'	73°34'	73°32'
SURFACE SALINITY ‰	33.00	35.33	—	—	—
SURFACE TEMPERATURE °C.	11.6	19.8	20.2	23.6	24.9

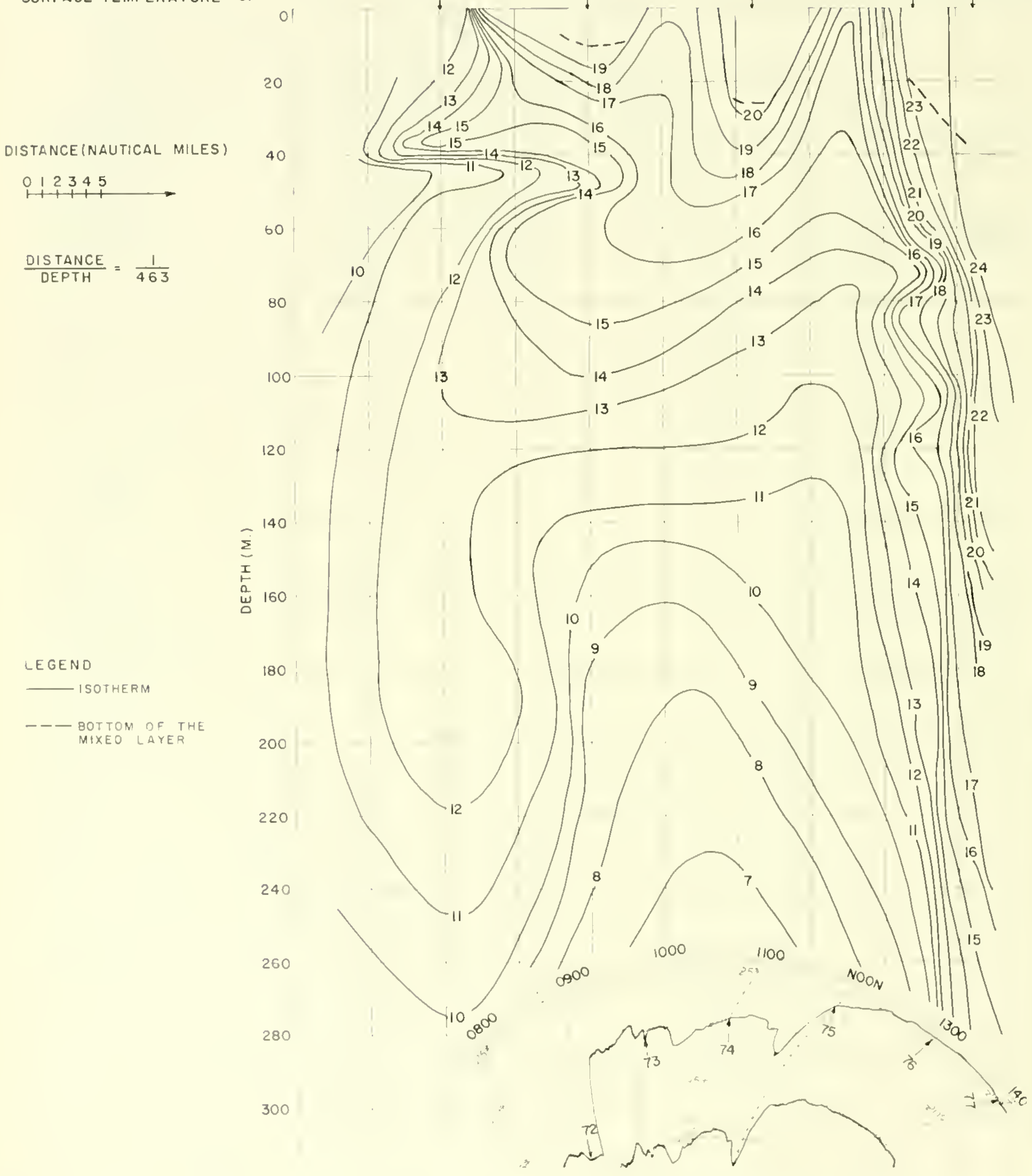


FIGURE 10.—Transect I—Section 8, May 15, 1963. (*See* caption for fig. 3.)

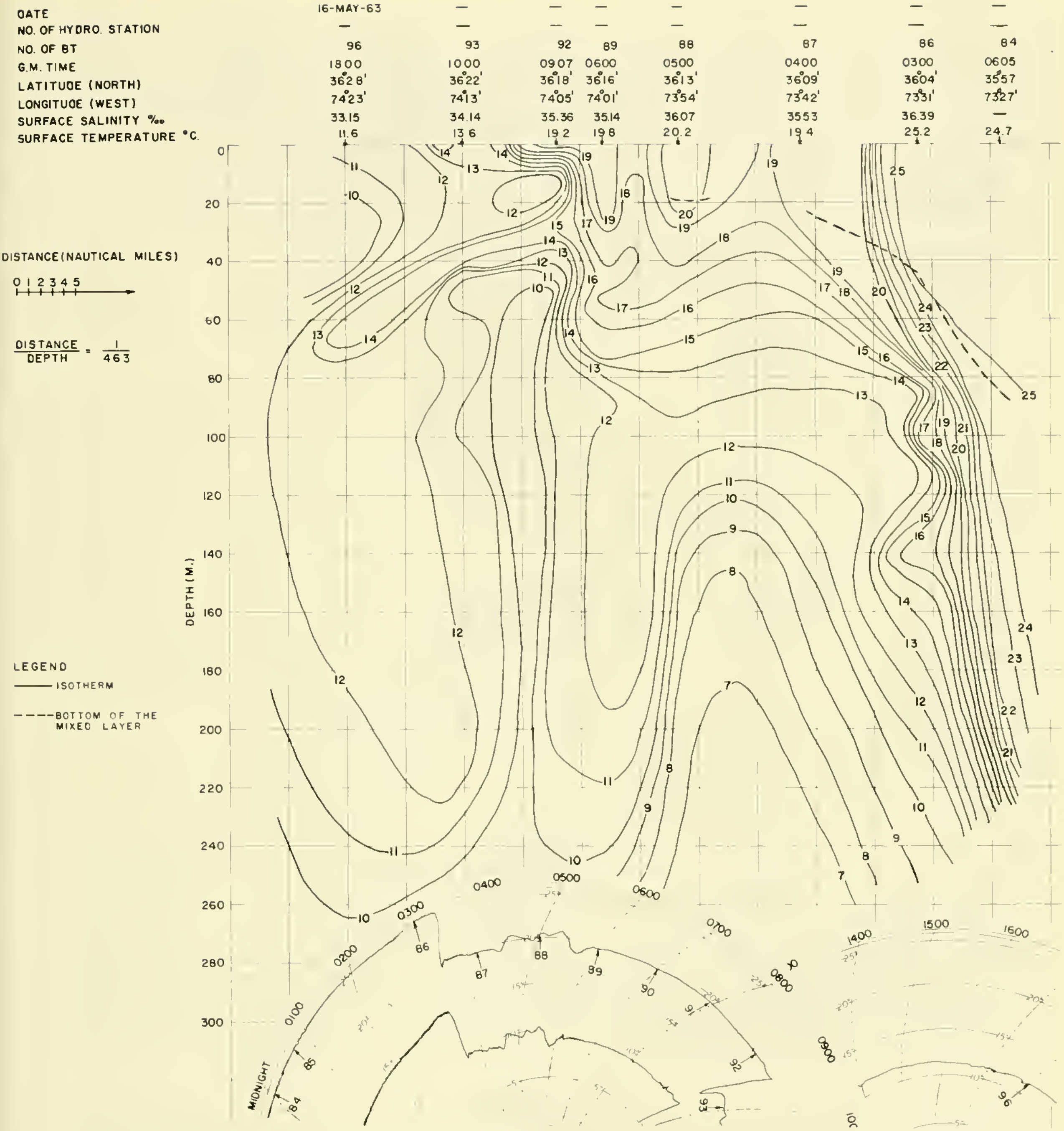


FIGURE 11.—Transect I—Section 9, May 16, 1963. (*See* caption for fig. 3.)

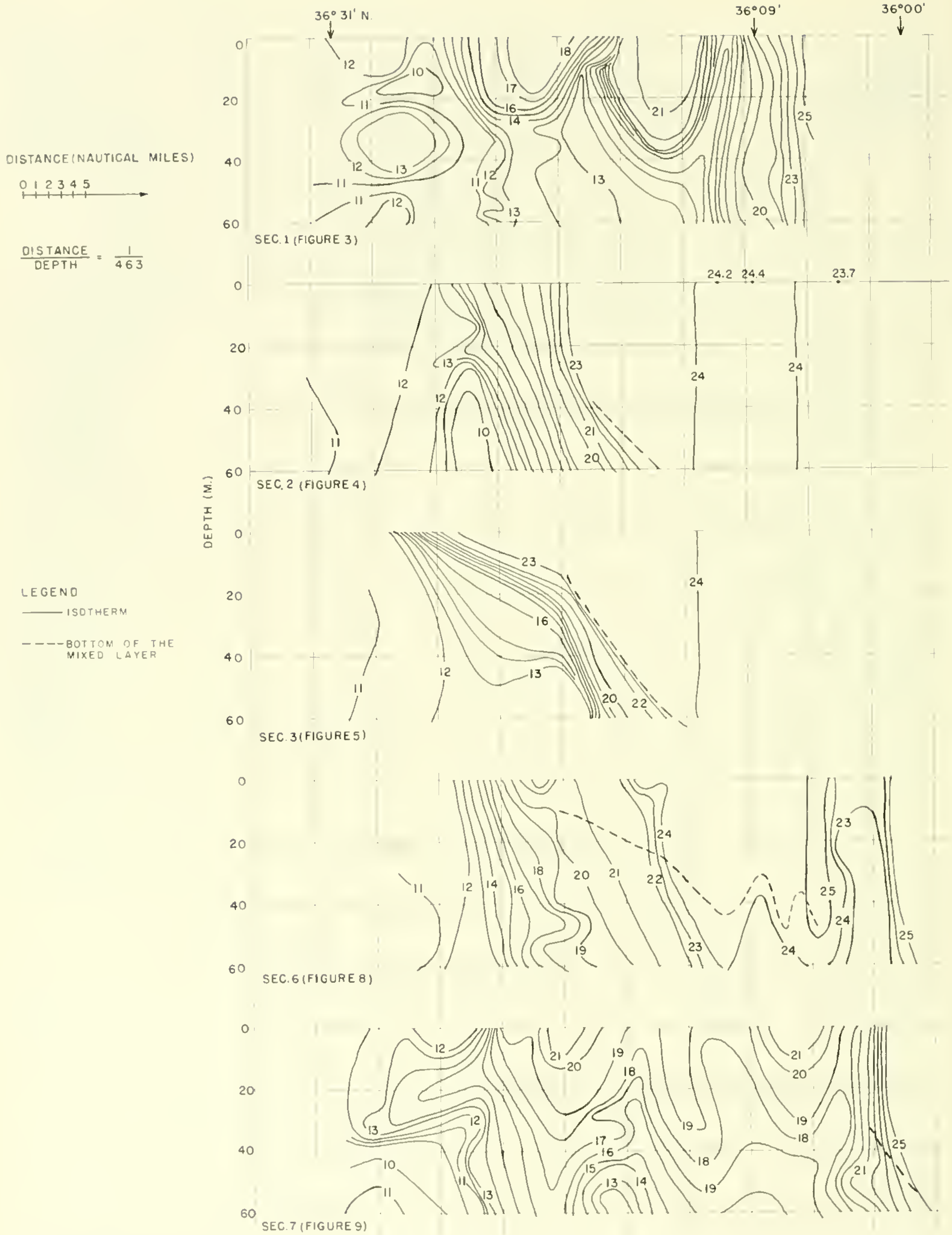


Figure 12.—Sections 1, 2, 3, 6, and 7 of transect 1, surface to 60 m., replotted with corresponding geographical points in approximate vertical alignment.

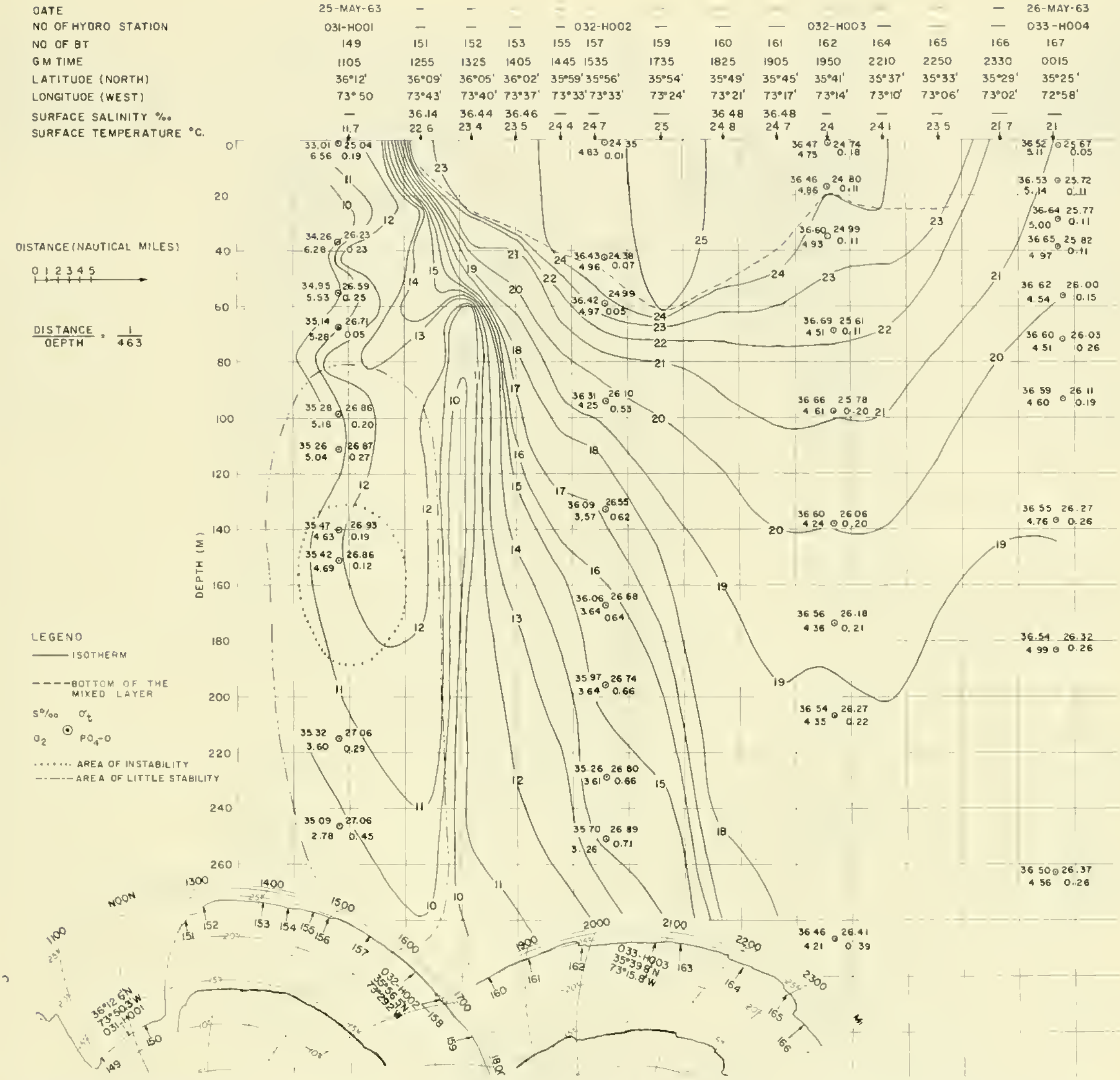


FIGURE 13.—Transect I—Section 10, May 25, 1963. Vertical temperature profile and thermograph record of surface temperatures. Thermograph temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers appear along the surface temperature trace to show the times of the casts. Data on salinity, density, dissolved oxygen (ml./l.), and inorganic phosphate (μg.-at./l.) are plotted on the vertical profile but not contoured.

the left boundary of the Gulf Stream in each transect is indicated in figure 1 by unbroken straight lines. The observed range of positions of the boundary on transects I and II is indicated by two parallel dashed lines. The mean and range of the boundary positions along transect I are based on observations during 14 crossings between May 10 and June 6, 1963, and along transect II on 5 consecutive crossings between May 31 and June 5, 1963. The range is not given along transect III because only three sections were made across the boundary (in 2 consecutive days).

Data are inadequate for the evaluation of horizontal movement of the left boundary or of the warm core between the transects. (Data from the only run along the boundary from transect II to transect I did not show significant meandering.) It is reasonable, nevertheless, to make inferences from transect I data,

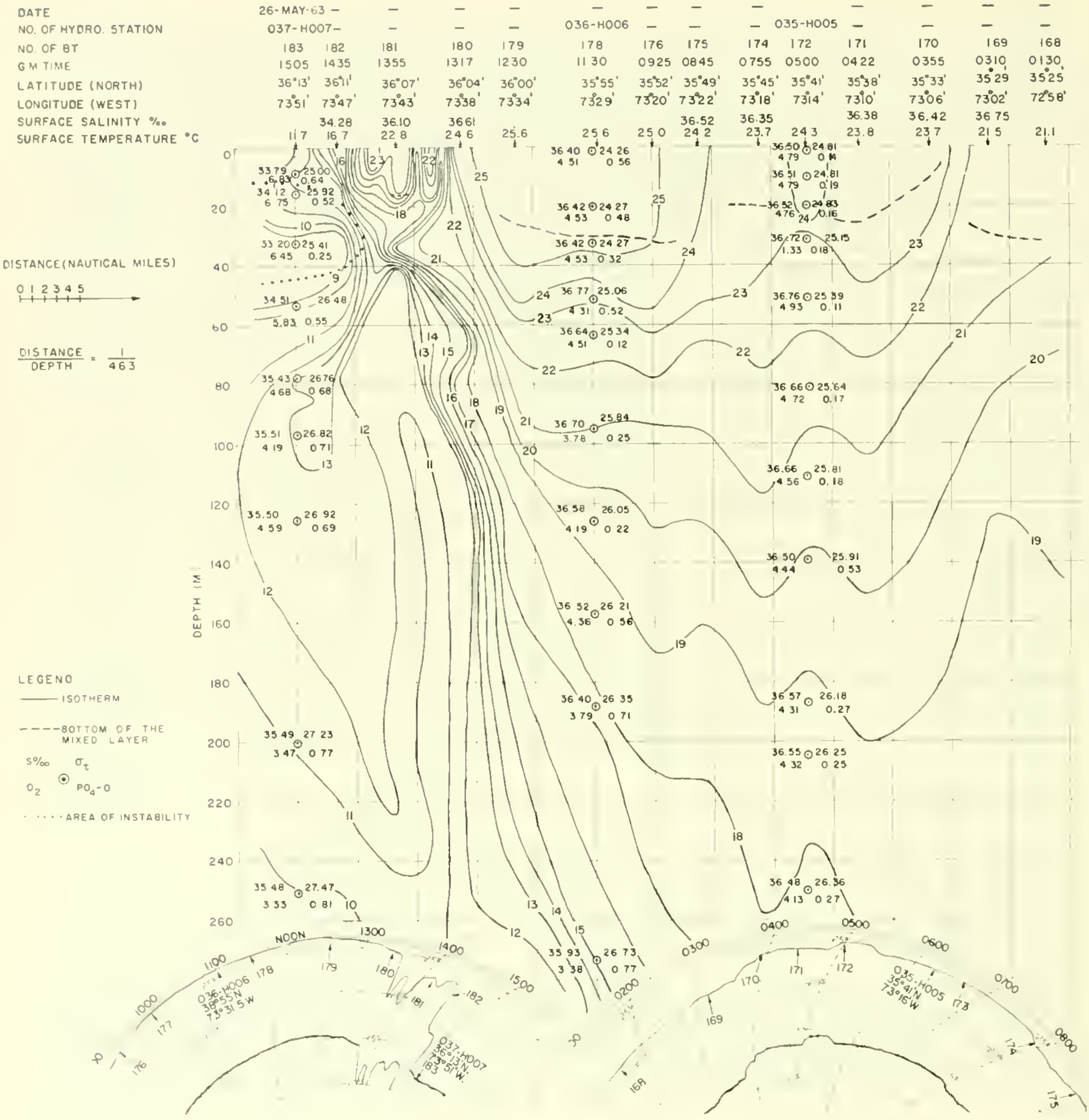


FIGURE 14.—Transect I—Section 11, May 26, 1963. (*See* caption for fig. 13.)

in which the position of the left side of the warm core oscillates by about 10 miles (18.5 km.) on either side of the mean (dotted line, fig. 1). The left boundary of the Gulf Stream was not more than 10 miles right of its mean position in any of the sections but was about twice as far left in one section.

The observations along transect I indicate that the oscillation of the left boundary of the Gulf Stream and the width of the intermediate zone were not directly interdependent. Formation of the intermediate zone did not necessarily depend on oscillation of the boundary—oscillation may presumably occur when the intermediate zone is nonexistent. Some boundary oscillations, however, did seem to be con-

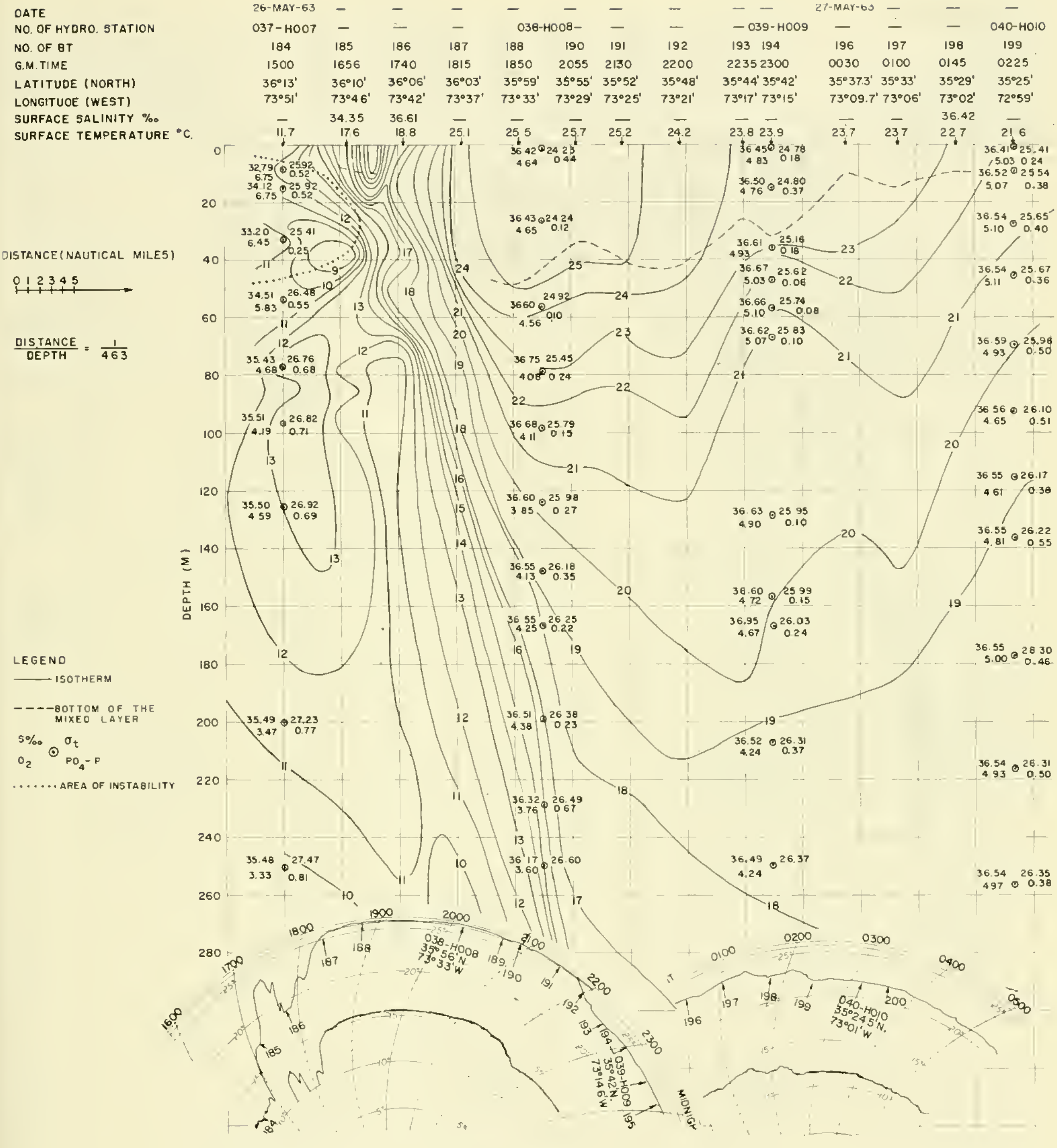


FIGURE 15.—Transect I—Section 12, May 26, 1963. (*See* caption for fig. 13.)

nected with development of an intermediate zone. The boundary during a well-developed intermediate zone was found right of its mean position, but the boundary during a weakly developed intermediate zone was left of its mean. Along transect II, the limited number of observations suggests that the pattern of oscillation was similar to that in transect I.

WARM CORE OF THE GULF STREAM

The core of warmest water was found at or near the left boundary of the Gulf Stream. The

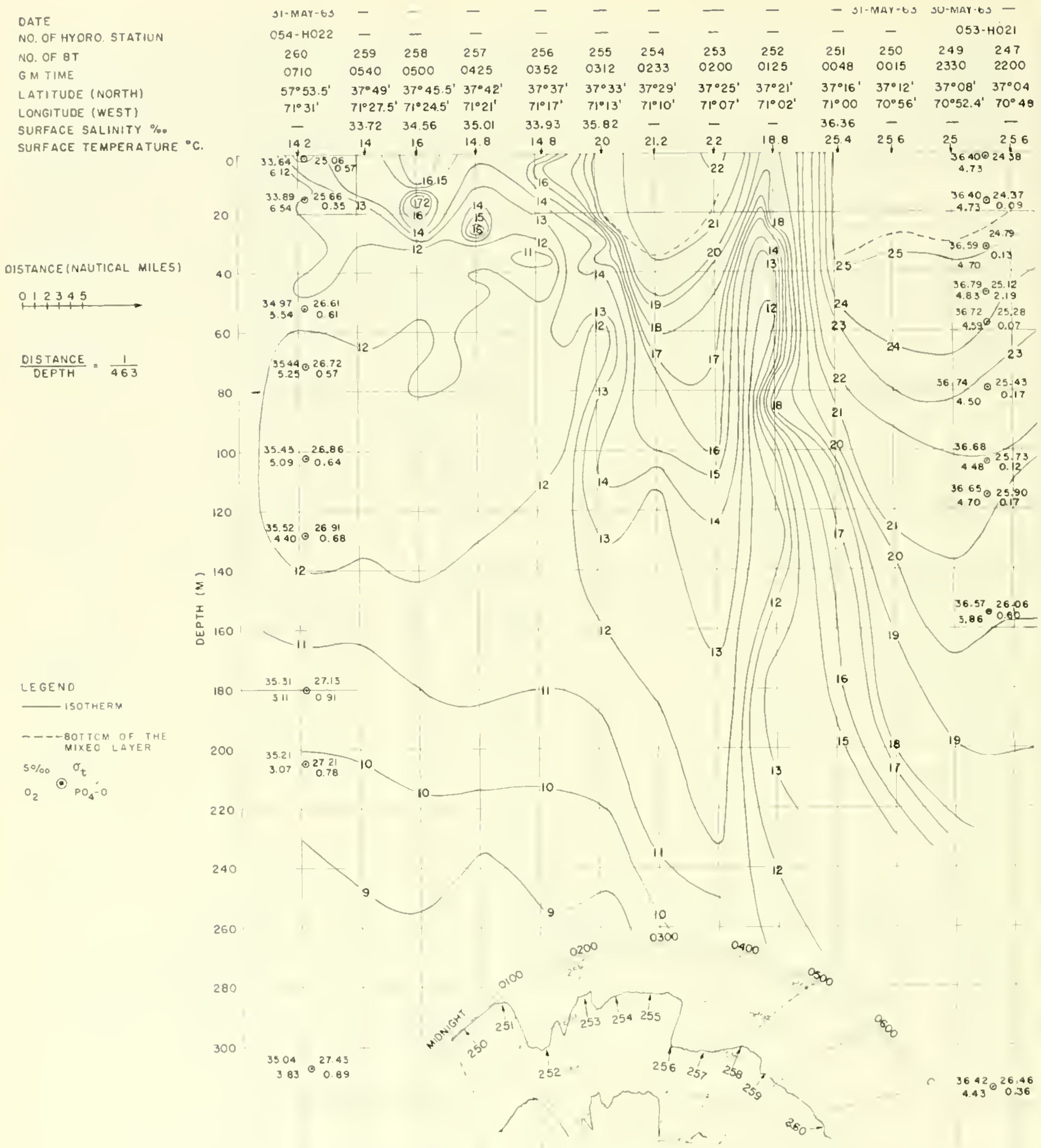


FIGURE 16.—Transect II—Section 13, May 31, 1963. (*See* caption for fig. 13.)

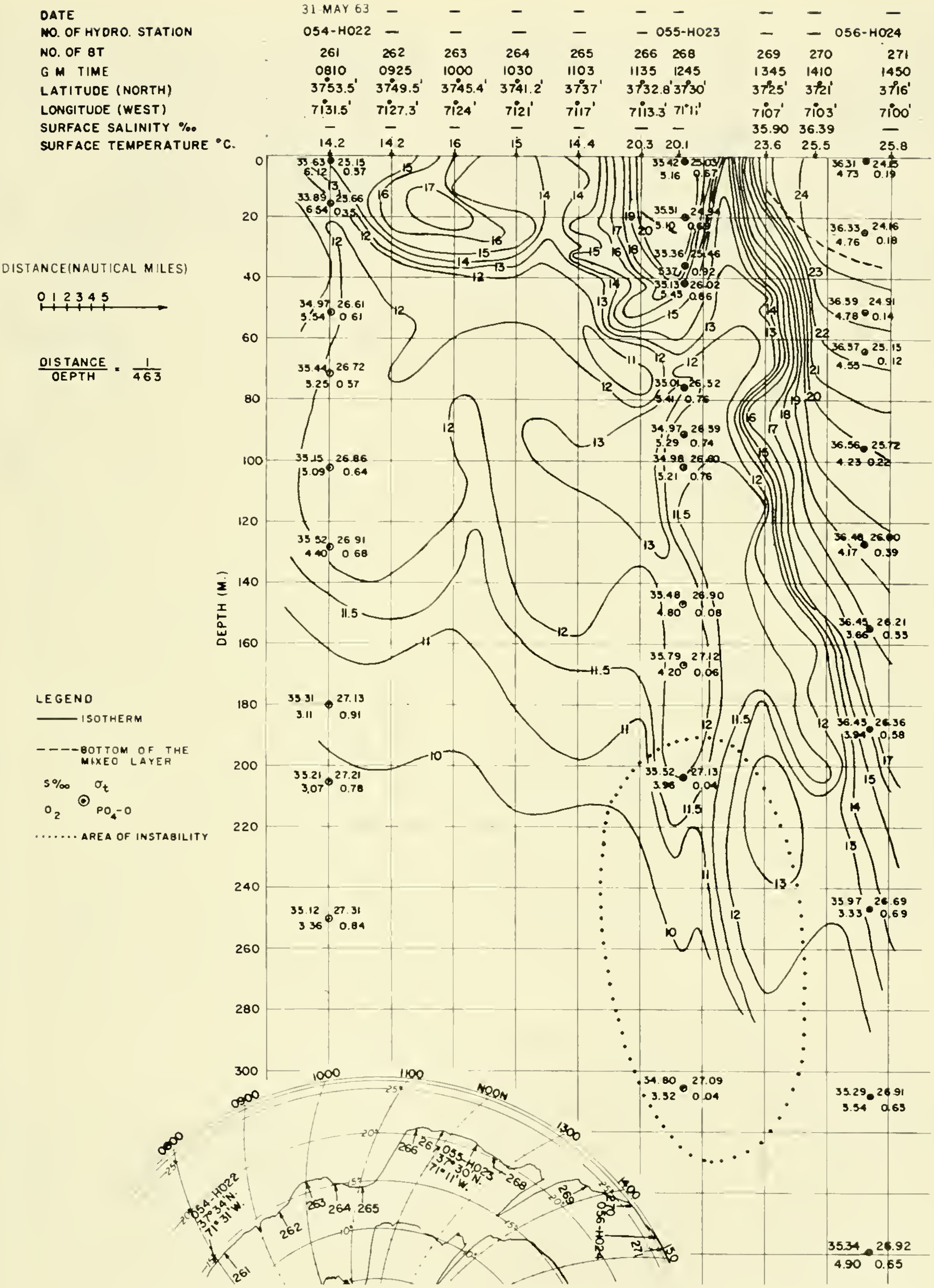


FIGURE 17.—Transect II—Section 14, May 31, 1963. (*See* caption for fig. 13.)

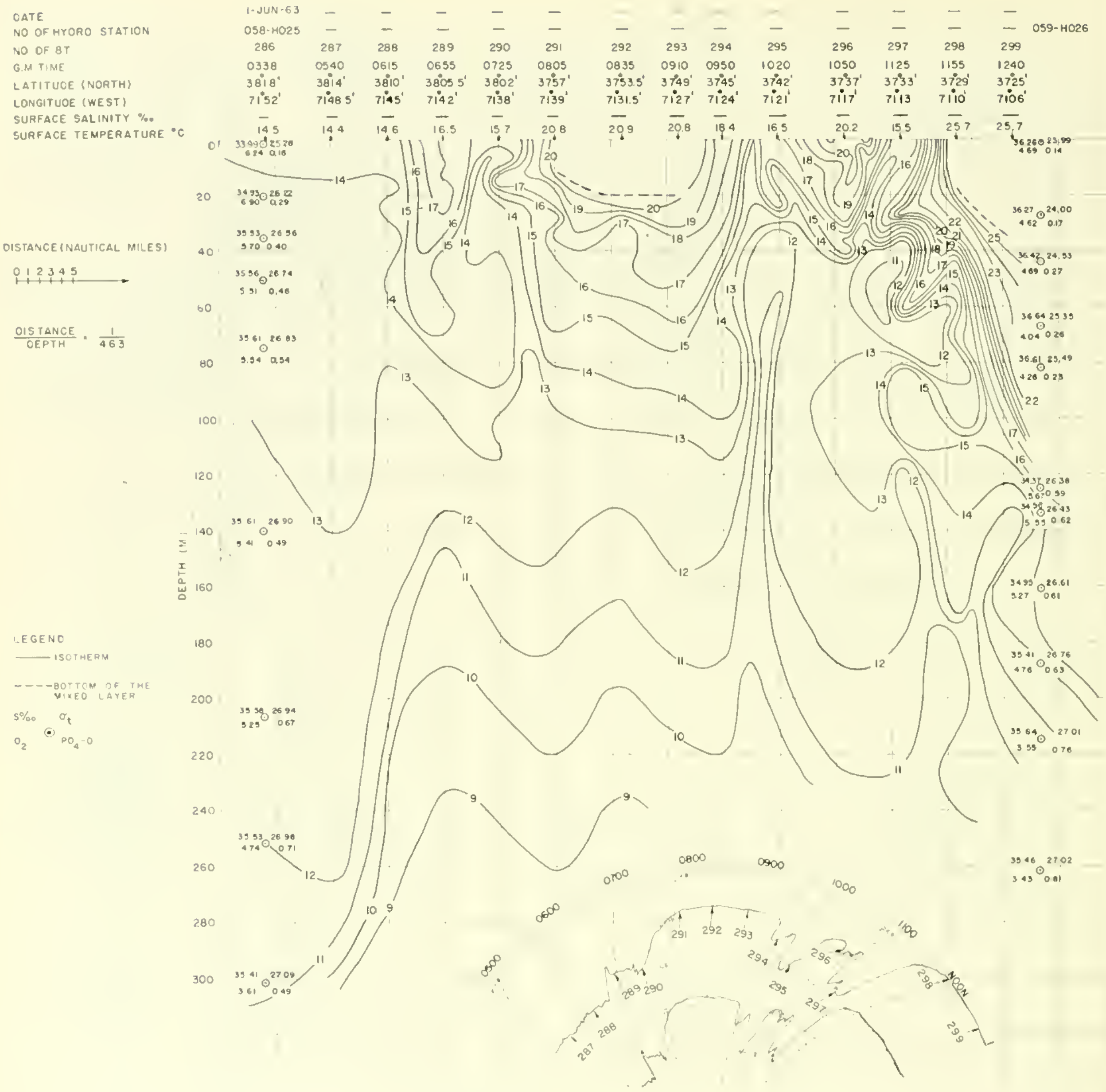


FIGURE 18.—Transect II—Section 15, June 1, 1963. (*See* caption for fig. 13.)

warm core is defined as that part of the Gulf Stream which was warmer than 21° C. in the period covered in this report.

RIGHT BOUNDARY OF THE GULF STREAM

The right boundary of the Gulf Stream is defined here as a strong horizontal temperature gradient at the surface as illustrated in figure 2 between BT's 367 and 366. The right boundary of the Stream was crossed three times along transect I. The mean position is indicated in figure 1 by a dash-dot line. Crossings were within a 2-day period, and the boundary was displaced slightly to the south on the third crossing. On the first crossing, the boundary appeared on the surface temperature record between BT's 165 and 166 (fig. 13); on the second crossing, between BT's 169 and 170 (fig.

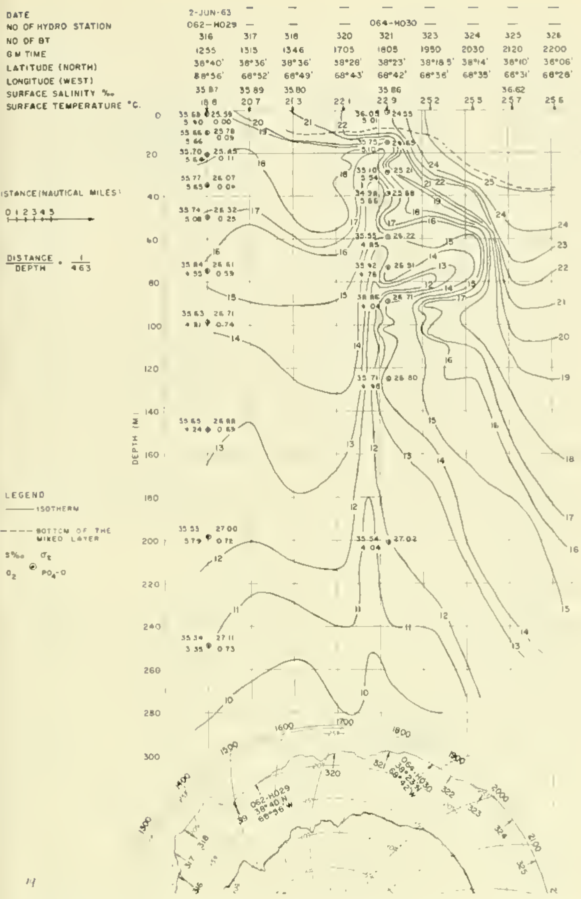


FIGURE 19.—Transect III—Section 16, June 2, 1963. (*See* caption for fig. 13.)

14); and on the third crossing, between BT's 197 and 199 (fig. 15).

The right boundary was crossed only once along transect II. Unfortunately, no surface temperatures are available because the recorder was temporarily out of order. Since the temperature difference between the Sargasso Sea and the Gulf Stream was 4° C., the boundary may have been even more distinct than along transect I.

The right boundary was crossed only once along transect III also; the crossing is shown on the surface temperature record between BT's 358 and 359 (fig. 21). The isolated peak on the trace represents an occasion when the ship was steered back and forth quickly across the boundary along legs about 200 m. long. At this time, the boundary was distinctly indicated by surface conditions. The sea was choppy on the Gulf Stream side but relatively smooth on the Sargasso Sea side, with no zone of transition—just a sharp line.

The right boundary was crossed again at lat. 37°12′ N. and long. 69°23′ W., while the vessel traveled from transect III to transect II (fig. 1; also see surface temperature trace in fig. 2). The boundary was crossed within 5 miles (9.3 km.). Since we were running obliquely to the Stream, the actual gradient at the boundary must have been considerably steeper than indicated on the trace.

The presence of a distinct right boundary on all occasions contradicts statements in the literature on the subject, to the effect that no detectable boundary exists between the Gulf Stream and the Sargasso Sea (Iselin, 1936, 1940). Possibly, of course, the boundary is not marked in the warm season, when the temperature of the surface waters is higher in the Sargasso Sea than in the Gulf Stream. Perhaps the right boundary is more typical of conditions in winter and spring than in other seasons.

WIDTH OF THE GULF STREAM

The Gulf Stream was about 50 miles (92.6 km.) wide along transects I and II, but about 70 miles (129.6 km.) along transect III. The greater width along transect III may not have represented a greater actual width of the Gulf Stream, but only a transient deformation of its right side. A similar deformation is indicated for the same day at this location in the U.S. Naval Oceanographic Office sea-surface temperature chart.

ENVIRONMENT OF THE GULF STREAM

The Gulf Stream structure, at the surface bounded on the left and right as defined in the previous section, consisted of a warm core flanked by rather small horizontal temperature gradients of varying widths. The warm core extended to depths of 60 to 80 m. over a width of 25 to 35 miles (46.3–64.8 km.). Mean values are given to facilitate comparison of the surface properties of the slope water, the Gulf Stream as a whole, the warm core of the Gulf Stream, and the Sargasso Sea (table 1). The slope water values are from five stations along transects I and II. None of these five stations was entirely out of Gulf Stream influence; therefore, the values are not entirely representative of typical slope water.

TABLE 1.—*Mean values of surface properties in the Gulf Stream and adjacent water masses (Geronimo Cruise I)*

	Temperature	Salinity	σt	Oxygen	PO_4–P
	° C.	‰		*ml./l.*	*µg. at./l.*
Slope water	12.98	33.59	25.34	6.31	0.35
Gulf Stream (all stations)	25.01	36.42	24.41	4.76	.18
Gulf Stream (warm core stations only)	25.61	36.36	24.20	4.66	.27
Sargasso Sea	21.64	36.57	25.49	5.08	.15

The water masses of the slope water, Gulf Stream, and Sargasso Sea were distinctly different in all properties, both at the surface and in the subsurface layers. The subsurface properties left of the Gulf Stream were characteristically erratic; in the Gulf Stream and Sargasso Sea the properties tended to be regular, except for phosphate, which varied greatly to about 300 m.

INTERACTION OF THE SLOPE WATER AND THE GULF STREAM

The present data draw special attention to the transient nature of the intermediate zone at the left side of the Gulf Stream. In the first section with oceanographic stations (transect I, fig. 13), one sharp boundary appears where the surface temperature increased from 13° to 22° C. in about 2.5 miles (4.6 km.); the intermediate zone was almost nonexistent at the surface. In the transect of 24 hours later (fig. 14), the situation has changed drastically: the intermediate zone extends over 15 miles (27.8 km.), and two surface temperature boundaries are distinct. The variability of the width of the intermediate zone and its intermittent disappearance tend to demonstrate that its existence was the result of interaction between two water masses.

INTERACTION SYSTEMS

The intermediate zone has, of course, a vertical dimension. In the following interpretation, therefore, it is convenient to use the term "interaction system" for the entire volume of intermediate water.

The dimensions, shape, and internal structure of the interaction system shown in figures 3 and 4 change and transform rapidly, but the formation of the system seems to have a certain repetitive pattern. In figure 3 the intermediate zone is well developed. The two boundaries, enclosing the intermediate zone, are clearly marked on the surface temperature record. Temperature increases sharply by 7° C. at the slope water boundary, between the BT numbers 4 and 5. The intermediate zone is composed of two cold-water belts and two shallow warm-water cores. At the boundary between the intermediate zone and the Gulf Stream the temperature rises in two steps from about 15° in the cold belt to 24° in the Gulf Stream. A complicated pattern of the interaction extends in this section to about 230 m.

When the next section (fig. 4) was taken 2 days later, the boundary structure had changed. The intermediate zone with shallow currents and cold-water bands disappeared. Only one boundary was at the surface between the slope water (temperature 11.6° C. and salinity 33.75‰) and the Gulf Stream (temperature 23.2° C. and salinity 36.29‰); within the warm core the temperature was 24.2° C. and salinity 36.41‰. Some traces in the interaction system can be observed in the subsurface. The surface temperature trace is relatively smooth along the steep temperature gradient in the boundary zone.

In the following section (fig. 5) the boundary was crossed about 6 hours later. The boundary zone is narrower than in the previous section. The temperature changes from 11.8° C. to 23° C. in about 4 miles (7.4 km.), and the surface temperature trace rises almost vertically, but, in general, the boundary structure does not change between the two sections. A large mass of 12° C. water is enclosed by cooler water in the subsurface.

The section in figure 6 shows the boundary about 5 hours later. The surface temperature trace shows a small disturbance within the boundary. The disturbance was not present in the previous section. In the subsurface the 12° C. water has been reduced in volume and has separated. A bubble of 13° C. water is at 45 m., but it is not certain whether it has been ad-

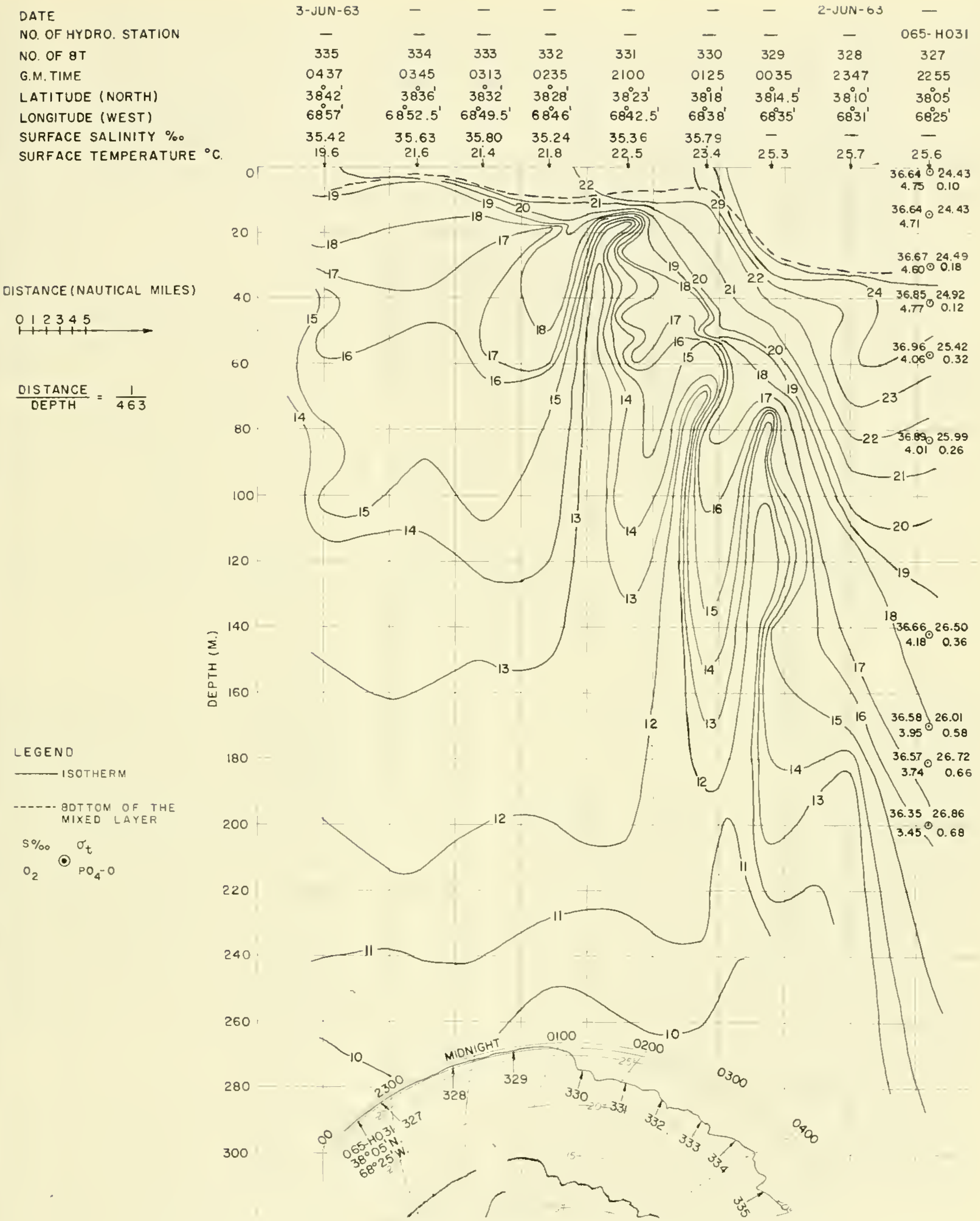


FIGURE 20.—Transect III—Section 17, June 3, 1963. (*See* caption for fig. 13.)

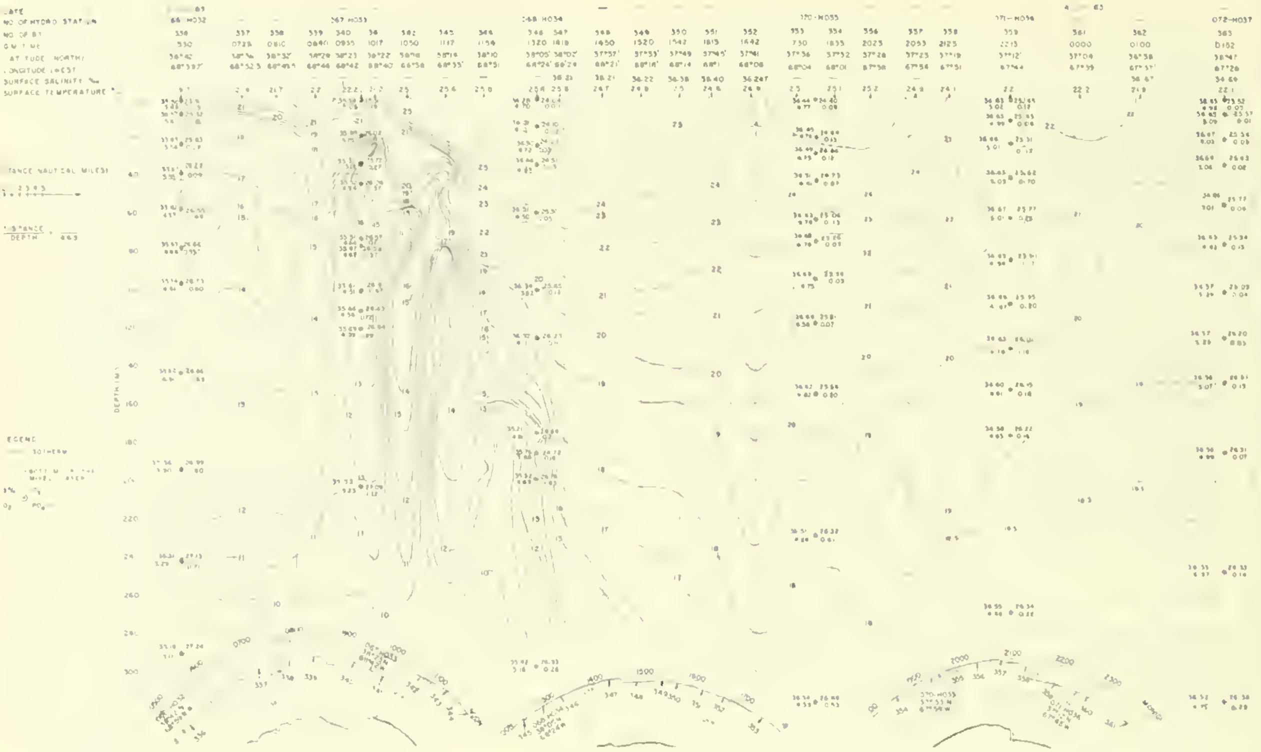


FIGURE 21.—Transect III—Section 18, June 3, 1963. (*See* caption for fig. 13.)

vected along the boundary or formed locally by occlusion of a lateral tongue of warmer boundary water.

About 7 hours later was the next crossing of the boundary (fig. 7). The boundary disturbance, which had just started in the previous section, had intensified and looked like a shallow small-scale upwelling with a cool belt very close to the Gulf Stream water. The surface temperature trace shows it as a cool-water stripe. The mass of 12° C. water in the subsurface has reduced further in volume. The warm bubble is at a shallower depth in this section than in the previous and is somewhat warmer. It may be either a new feature or a slow drifting of the same occluded warm water along the boundary. We could expect such an elongated bubble to be warmer in the center.

In the following section (fig. 8) about 5 hours later, a very large-scale process begins within the left side of the Gulf Stream. The former boundary is at about the same location, and the small-scale disturbance is still clearly marked on the surface temperature trace. A new boundary is forming 25 miles (46.3 km.) within the Gulf Stream near the velocity maximum. The cool belt at the surface is shown at the right section of the temperature record at BT number 65. The surface salinity in the cool stripe is 36.04 ‰ and, probably, is somewhat lower in its center. To the left and to the right of the cool band the surface salinities are 36.37 ‰ and 36.37 ‰. The bottom of the mixed layer is indicated by the dashed line. The cool band has no mixed layer. Apparently an intense upwelling process has been just started and is cutting off a very large portion of the Gulf Stream water from the main body of the Stream.

The next section shown in figure 9 was made about 20 hours later. The intermediate zone is about 35 miles (64.8 km.) wide and is at about the same stage of development as it was in the first section (fig. 3). The separated mass at the Gulf Stream is split into two shallow warm-water cores. The subsurface has changing jets or tongues of cold and warm water immediately

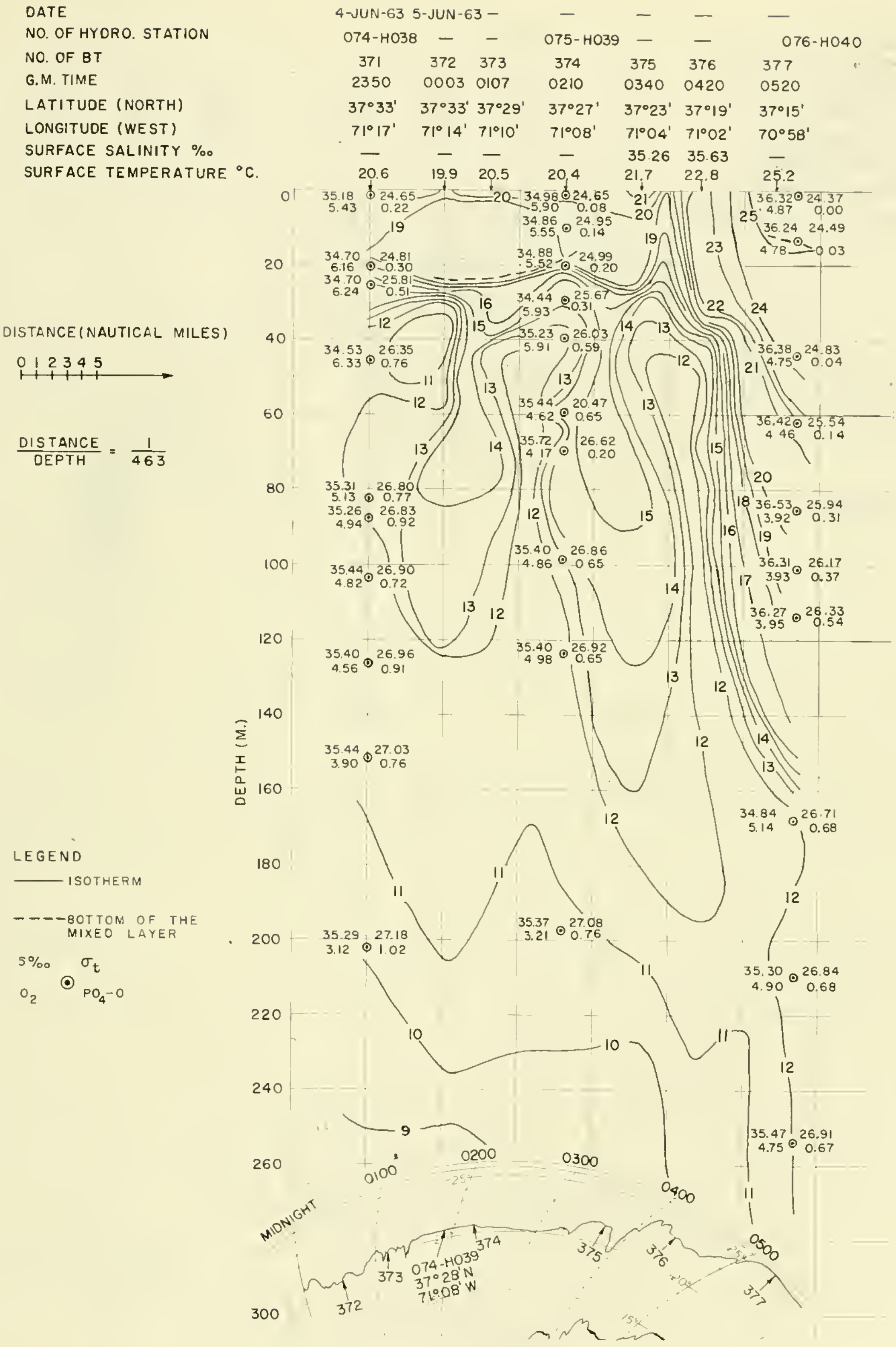
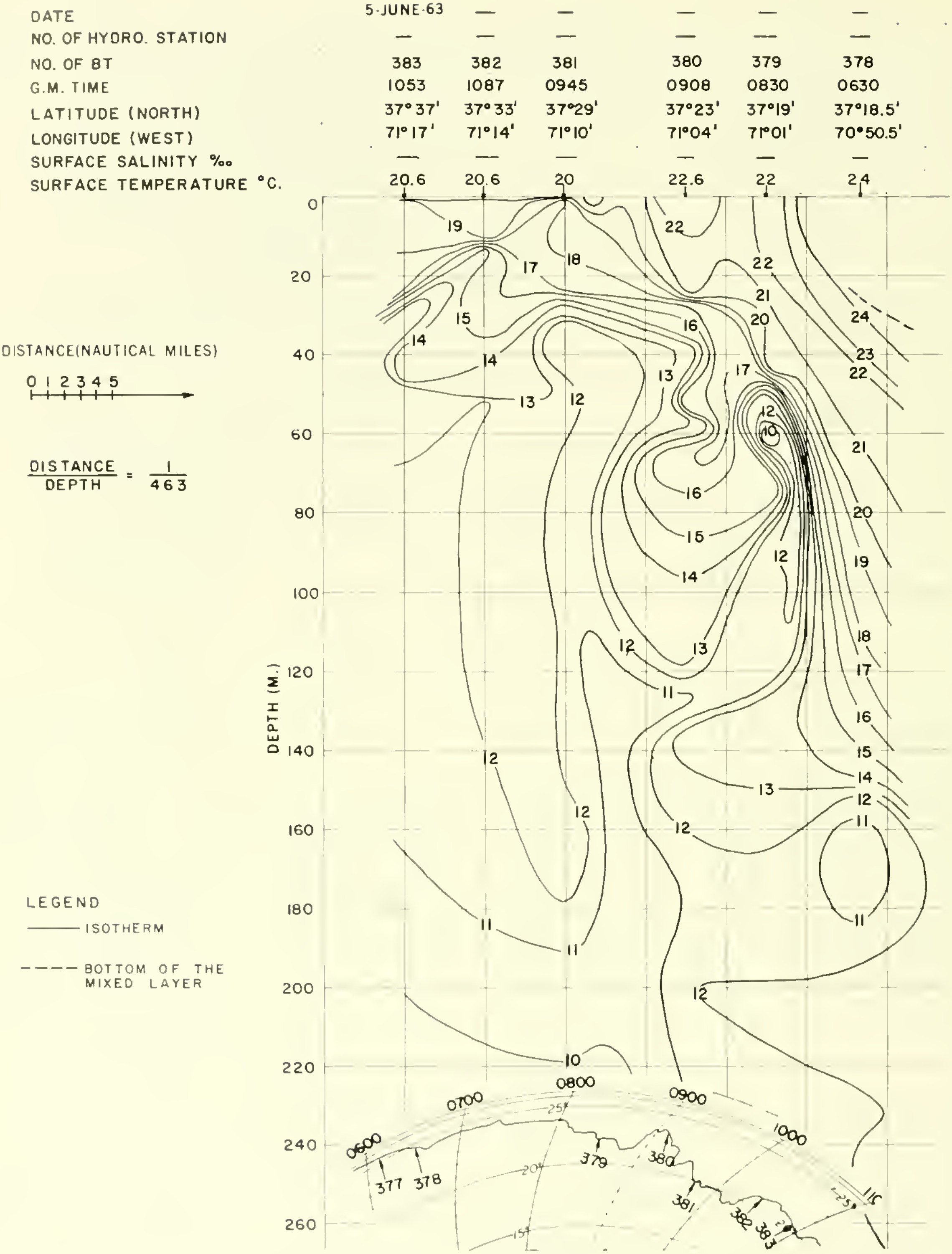


FIGURE 22.—Transect II—Section 19, June 4, 1963. (*See* caption for fig. 13.)



DATE	5-JUNE-63	—	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—	—
NO. OF BT	383	382	381	380	379	378
G.M. TIME	1053	1087	0945	0908	0830	0630
LATITUDE (NORTH)	37°37'	37°33'	37°29'	37°23'	37°19'	37°18.5'
LONGITUDE (WEST)	71°17'	71°14'	71°10'	71°04'	71°01'	70°50.5'
SURFACE SALINITY ‰	—	—	—	—	—	—
SURFACE TEMPERATURE °C.	20.6	20.6	20	22.6	22	24

FIGURE 23.—Transect II—Section 20, June 5, 1963. (*See* caption for fig. 13.)

DATE	6-JUN-63	—	—
NO. OF HYDRO. STATION	—	—	—
NO. OF BT	398	399	400
G.M. TIME	0145	0215	0247
LATITUDE (NORTH)	36°13'	36°09'	36°06'
LONGITUDE (WEST)	73°49'	73°45'	73°41'
SURFACE SALINITY ‰	32.55	32.04	—
SURFACE TEMPERATURE °C.	16.3	16	26

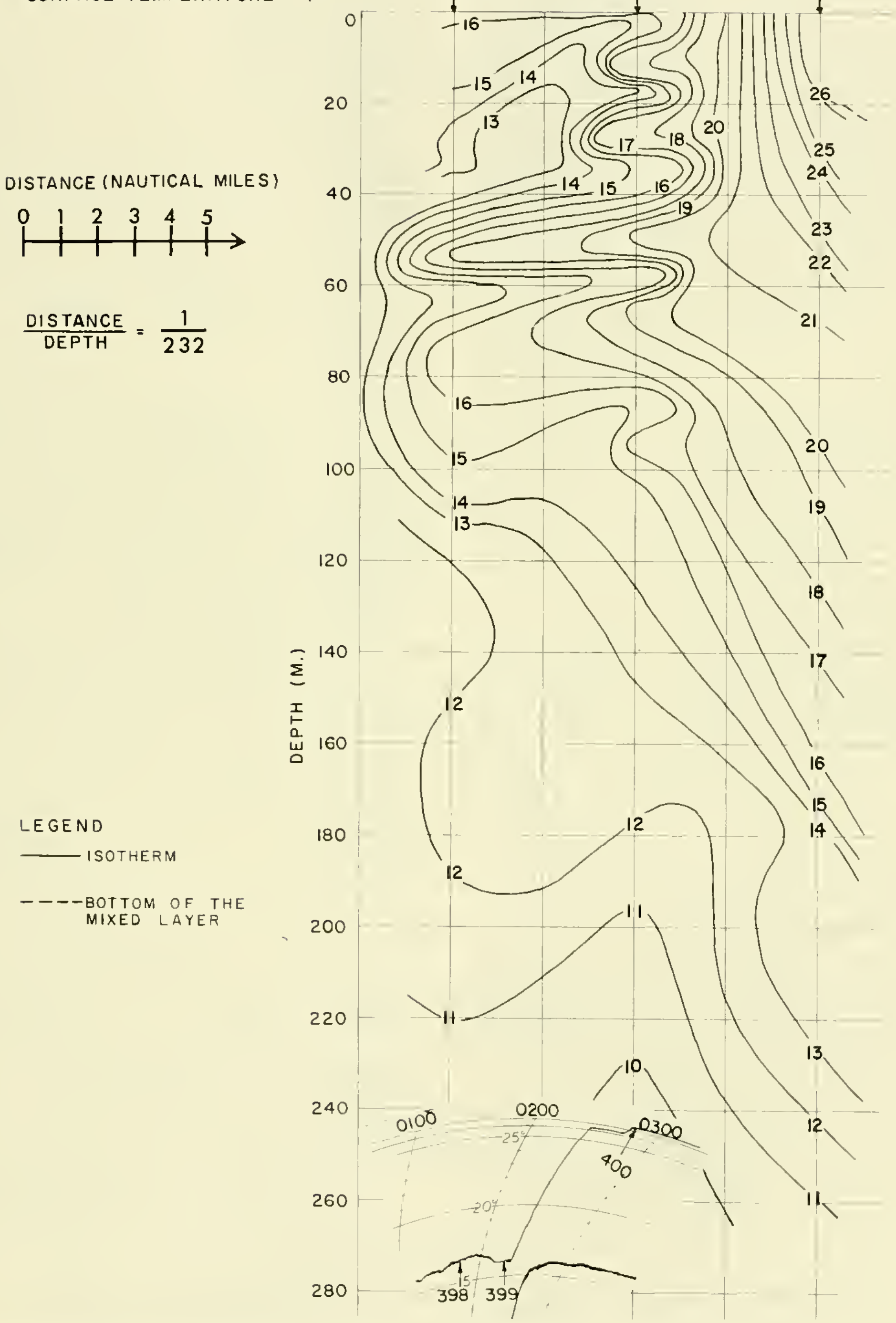


FIGURE 24.—Transect I—Section 21, June 6, 1963. (*See* caption for fig. 13.)

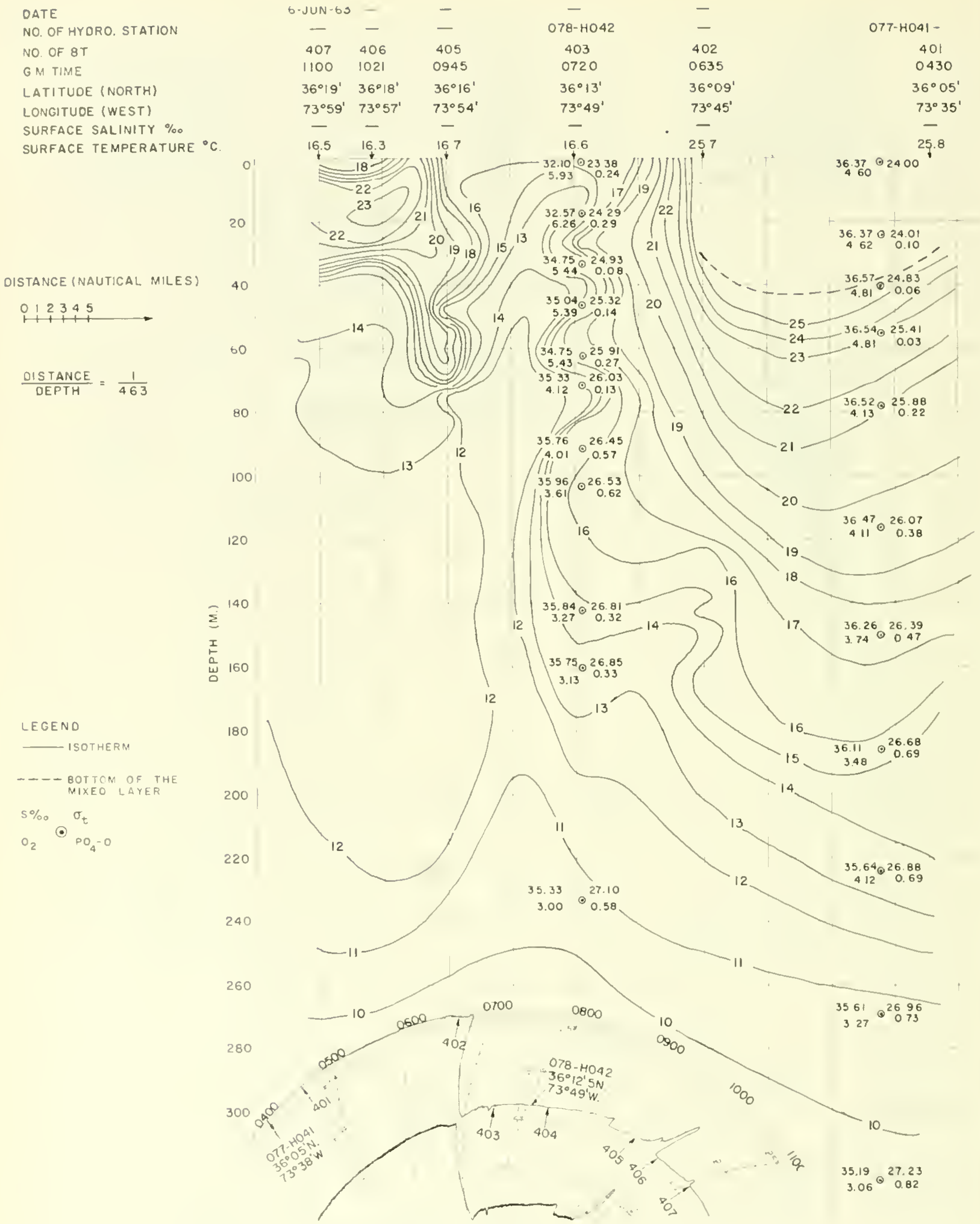


FIGURE 25.—Transect I—Section 22, June 6, 1963. (*See* caption for fig. 13.)

to the left of the slope water boundary at the surface.

The section shown in figure 10 was taken about 5 hours later, and one more section of the sequence was made 20 hours later (fig. 11). Both sections represent a dissipation stage of the interaction system which has been formed by the process shown in figure 8.

The thermal structure in figure 10 is somewhat simpler than in the previous section (fig. 9), but the two cold-water stripes, one near the Gulf Stream boundary and the other between the two shallow warm-water cores, are still very well marked on the surface temperature trace. The cold-water stripes are almost eliminated in the next section (fig. 11). The surface temperature is relatively smooth between the two steep temperature gradient zones at the boundaries on both sides of the intermediate zone.

A number of the sections indicate that the Gulf Stream boundary moved to the left during the absence of an interaction system. To illustrate this movement, the upper 60 m. of five of the sections from transect I were replotted (fig. 12), and corresponding geographic points were placed in approximate vertical alignment. (Full plots of these sections appear in figures 3, 4, 5, 8, and 9.) These sections start during one interaction cycle and end during the succeeding cycle, 4½ days later. Because the first and last of these sections represent about the same stage in the successive cycles, the time of a cycle from one strong and well-developed interaction system to another was about 4½ days (108 hours).

When the intermediate system decayed, the Gulf Stream boundary moved to the left and just one boundary remained. It became the slope water boundary when the new Gulf Stream boundary developed near lat. 36° N. The slope water boundary is almost exactly at the same location as it was in the previous cycle (fig. 3), but the new Gulf Stream boundary is about 6 miles (11.1 km.) farther to southeast and the intermediate zone is wider.

The next section across the Gulf Stream, along transect I (fig. 13), was made 10 days later. Oceanographic stations and BT's were taken in this and all the following sections. There was no intermediate zone, and the left boundary of the Gulf Stream corresponds to the situation in section 3 (fig. 5); however, this time the single boundary is about 24 miles (44.4 km.) to the southeast. Time interval between sections 3 and 10 was about 278 hours. If two cycles occurred during this time, the average period would be 139 hours.

Over half the cycle of a small interaction system was also recorded in three sections on transect I (figs. 13, 14, and 15). These figures suggest that about half the cycle was completed in 30 hours. This timing is in reasonable agreement with the 108-hour period estimated above for the cycle of a larger interaction system. Presumably the time of a cycle may vary considerably. The life span of an interaction system probably depends less on volume and shape than on the energy it contains after the separation stage.

The sections along transect II (figs. 16, 17, and 18) show stages in the maximum development of another strong interaction system. The three sections record such a small part of a complete cycle, however, that the duration of that cycle cannot be estimated.

The appearance of a rather weak interaction system can be detected in the sections along transect III (figs. 19, 20, and 21).

Altogether, six different interaction systems were observed during the *Geronimo* cruise. The mean cross-sectional area of the Gulf Stream water occluded into them is estimated to have been 1.69 x 10^6 m.^{2}

DIRECTION AND VELOCITY OF FLOW

Beginning at the stage of development shown in figure 8, the interaction system is cut off from the body of the Gulf Stream and acts independently. It presumably flows in the same general direction as the Gulf Stream, but the cold stripe that separates the interaction system from the Gulf Stream may have some tendency toward an opposite flow. This tendency is probably only occasionally strong enough to overcome opposing flow from both sides, induced by the horizontal shearing stress. Vertically, the cold stripes and the whole interaction system sometimes seem to extend to depths greater than 300 m. but many sections indicate that the rapid change of properties occurs above 300 m. (figs. 3, 16, 17, 18, and 22).

The geostrophic velocity computed with reference to 600 m. between stations 054–HO22 and 055–HO23 (fig. 17) was 23 cm./sec. The velocity must be considerably greater in the warm-water core of the interaction system (between hydrographic station 055–HO23 and the location of BT number 266, for example). The mean geostrophic velocity, with reference to 600 m. between stations 054–HO22 and 056–HO24, was 60 cm./sec, and between stations 055–HO23 and 056–HO24, it was 128 cm./sec. Because station 056–HO24 was located in the warm core of the Gulf Stream, the data are not applicable to the evaluation of energy left in the interaction system. The 600-m. reference level may be satisfactory for stations 054–HO22 and 055–HO23 but not for station 056–HO24. Additionally, this station is on the Gulf Stream side of the cold stripe. The mean geostrophic velocity computed between stations 054–HO22 and 055–HO23 appears realistic. No great velocities within the interaction systems were observed from the *Geronimo*.

PROCESS OF INTERACTION

Apparently Gulf Stream water was supplied to the interaction systems in two principal ways. During the present observations, the dominant supply was furnished by separation. A large volume of water is separated from the left flank of the main body of the Gulf Stream —for example see figure 8.

A supplementary supply of water was by injection. Tongues of warm and cold water alternating vertically extended over a considerable horizontal distance (fig. 24). The injections tended to be moderate to weak when the main interaction system was strong (figs. 8 and 16); conversely, the injection tongues tended to be actively developed when the main interaction system was nearly dissipated (figs. 10 and 11). A general idea of the dimensions of the warm-water tongues can be obtained from a profile based on BT observations along the slope water of the left boundary of the Gulf Stream, between transects I and II (fig. 26). The figure, which covers a distance of 140 miles (259.3 km.), shows one well-developed, warm-water tongue and a few cold tongues. The well-developed tongues were about 30 miles (55.6 km.) wide (parallel to the Gulf Stream boundary) and about 40 m. thick (vertical dimension) near the base. Their average projection was about 8 miles (14.8 km.) in the direction normal to the boundary, as evaluated from 11 well-developed examples in various sections. Gulf Stream water was not a contributing factor to numerous other tongues that seemed to have developed within the interaction system after separation (figs. 9 and 10).

DEVELOPMENT AND DISSIPATION

Two principal questions may be asked regarding the interaction systems: How or why do they develop, and what happens to the water mass separated from the Gulf Stream? When an interaction system had dissipated at the surface—whatever its dimensions or character —there remained just one sharp surface boundary between the slope water and Gulf Stream (figs. 5 and 13). It seems, however, that in depths from about 40 to 200 m., the interaction systems persisted for longer periods; possibly they never decayed completely. The sequence shown in figures 4 through 8 reveals that the remnants of an old interaction system appear to be absorbed by a new one. If volumes of water as large as those involved in interaction systems are disposed of by absorption within the neighboring water masses, perceptible changes in the character of these masses could be expected. Yet in our repeated sections along transect I (in a 1-month period), even though several interaction systems developed and dissipated, no appreciable change of properties was observed in the adjacent Gulf Stream and slope water. A small rise in temperature in the slope water can be attributed to heating as the warming season progressed. Slope water was less distinctly uniform at transect II than at transect I, but because the observation period was comparatively brief, no definite conclusions can be reached about the persistence of properties.

The slope water was warmer—by about 2° to 3° C.—at transect III than at transect I. The multistream structure of the Gulf Stream as represented by Fuglister (1951) was probably absent at transect I, but may have been start-

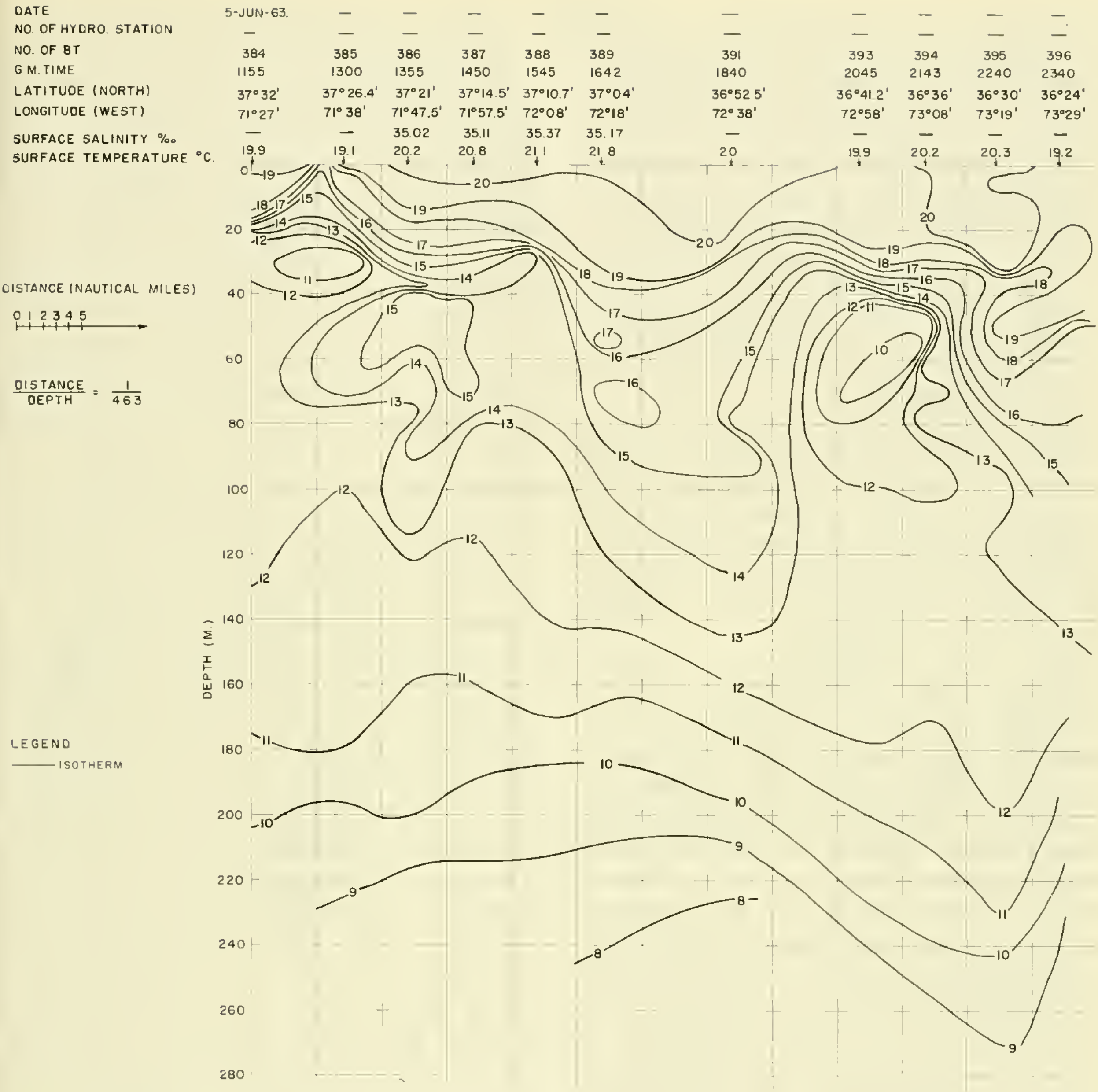


FIGURE 26.—Vertical temperature profile along the left boundary of the Gulf Stream between transects I and II.

ing to develop in the area between transects II and III. Thus, the likelihood exists that, in the process of dissipation, at least part of the mass of the interaction systems seen in the general area of transects I and II was channeled into secondary streams, and that these streams developed farther downstream into a multistream complex.

RETURN OF MIXED WATER TO THE GULF STREAM

A considerable part of the mass of a dissipating interaction system may be returned to the main body of the Gulf Stream at deeper levels than its point of origin. This assumption is supported by the fact that water properties in the interaction systems at depths of about

120 to 170 m. were generally the same as within the left side of the Gulf Stream at depths of 300 to 600 m. This similarity is illustrated in figures 27 to 30, which show temperature-salinity curves for the oceanographic stations made in sections 10, 12, 13, and 19. Coincidence of properties started at about $\sigma_t = 27.0$ and continued to the end of the curves (a little below 600 m.) where the approximate value is $\sigma_t = 27.8$. (The properties at 600 to 700 m. in the right side of the Gulf Stream and in the adjacent Sargasso Sea were entirely different—see the T–S curves of stations 051–HO19 and 052–HO20 in figure 27.)

The mean upper level of water with coinciding properties, computed from all available sections, was 355 m. for the left side of the Gulf Stream and 154 m. for the interaction systems. The horizontal distance between the generation area in the interaction systems and the locations of similar water in the Gulf Stream was 15 to 40 miles.

Most of the interchanging cold and warm tongues observed in the boundary area and in the interaction system were stable. When unstable situations do occur in the ocean, they are usually of short duration and it is difficult to obtain data on their frequency and the volumes. Unstable mass distributions may be created either by caballing or by rapid overflow of water of greater density over water of lesser density in the process of strong, lateral mixing. Oceanographic stations 031–HO01, 037–HO07, and 055–HO23 illustrate such unstable situations (figs. 13, 15, and 17). The instability, even if very limited in volume, was evident in 3 out of the 10 stations for which salinity data were obtained in the intermediate zone, whereas the total number of oceanographic stations was 42. The proportions may indicate that volumes of water exhibiting unstable mass distribution frequently occurred but lasted for only a brief period. Certainly errors in the data have to be considered; however, the three cases of instability occurred in the zone of intense interaction and none was outside of that zone. This fact indicates that the unstable situations were probably real.

ZONES OF CONVERGENCE AND DIVERGENCE

The left side of an interaction system is a zone of convergence with a rather permanent downward motion. When an interaction system dissipates, the convergence zone may be expected to move close to the left side of the Gulf Stream boundary. Downward motion caused by convergence is probably locally limited and too weak to transfer significant mass from an interaction system to the Gulf Stream. A superimposed momentum due to transient unstable mass distribution may, however, produce a downward flow strong enough to cover the horizontal distance between the generating and the discharging areas. The descending dense water would be absorbed by the left side of the Gulf Stream at levels about 200 m. lower than its point of origin in the interaction system. The downward motion, in turn, would intensify the surface convergence and, thus, produce a significant cross-current velocity component in the left side of the Gulf Stream.

The mean distance from the left boundary of the Gulf Stream to the location of maximum velocity in the Gulf Stream was 22 miles (40.7 km.), derived from four sections of surface velocity distribution across the current (Von Arx, 1952; Worthington, 1954). The distance between the right boundary of the Stream and the location of maximum velocity was 36 miles (66.7 km.). Outcroppings of cool water were present about 25 miles (46.3 km.) from the left boundary of the Stream, as can be seen from sections 3 and 6 (fig. 12) or by comparing sections 4 and 5 (figs. 6 and 7) with sections 6 and 7 (figs. 8 and 9). Thus, the cold stripe probably developed in the region of maximum velocity in the Gulf Stream, above the right flank of the steeply sloping isotherms, about where the 18° C. isotherm crossed the 200–m. level in section 5 (fig. 7).

Because of a strong cyclonic shear at the left of a velocity maximum and a slightly weaker anticyclonic shear at its right, a maximum horizontal gradient of the vertical component of absolute vorticity may be expected in the region of maximum velocity. The strong horizontal change in absolute vorticity may cause a tendency to diverge. If convergence in the area of interaction were intensified through the

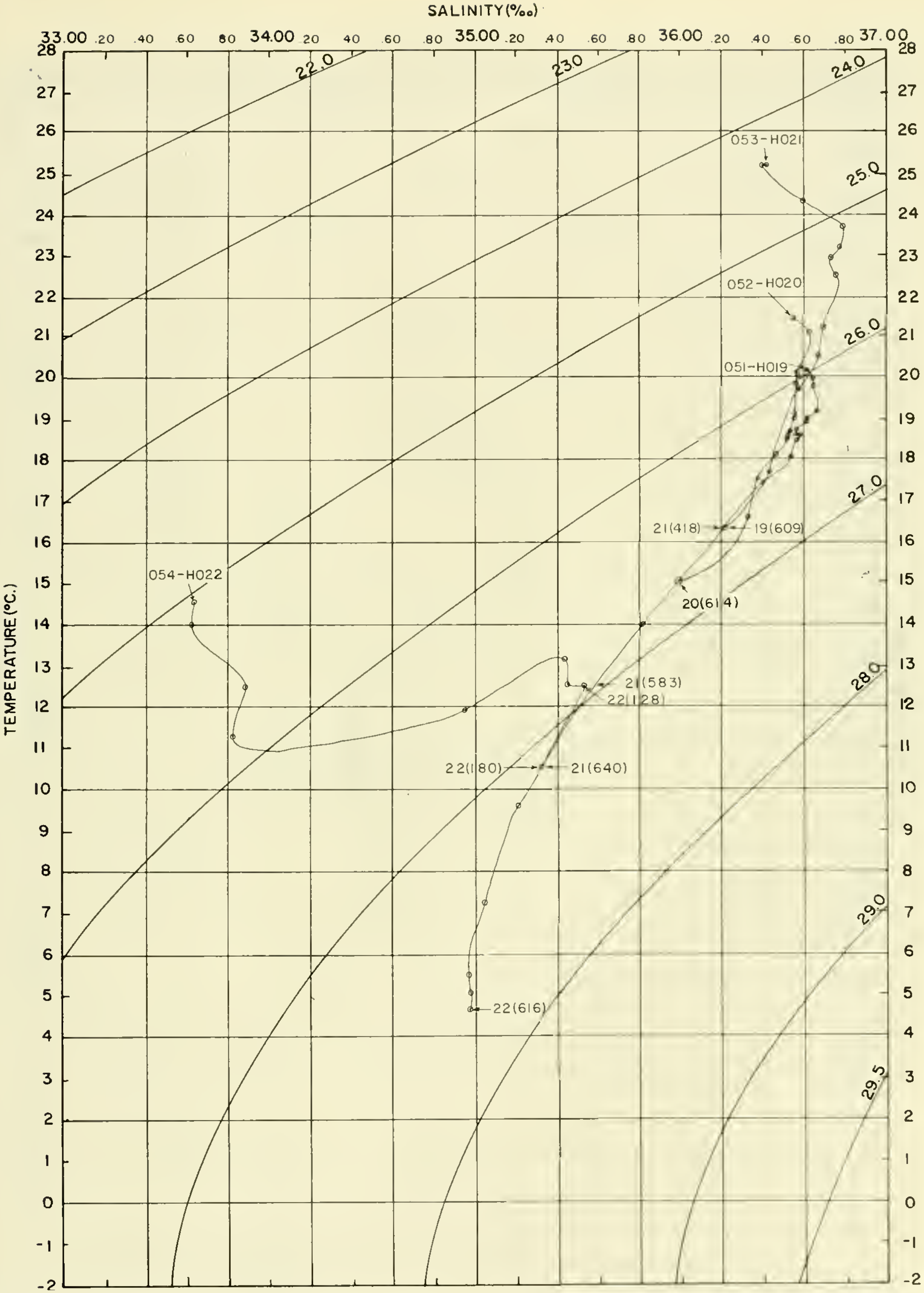


FIGURE 27.—Temperature–salinity curves along section 13. The hydrographic station number is indicated at the top of each trace. The last two digits of these station numbers also appear at points where the traces come close together or coincide. The depths of these points appear in parentheses.

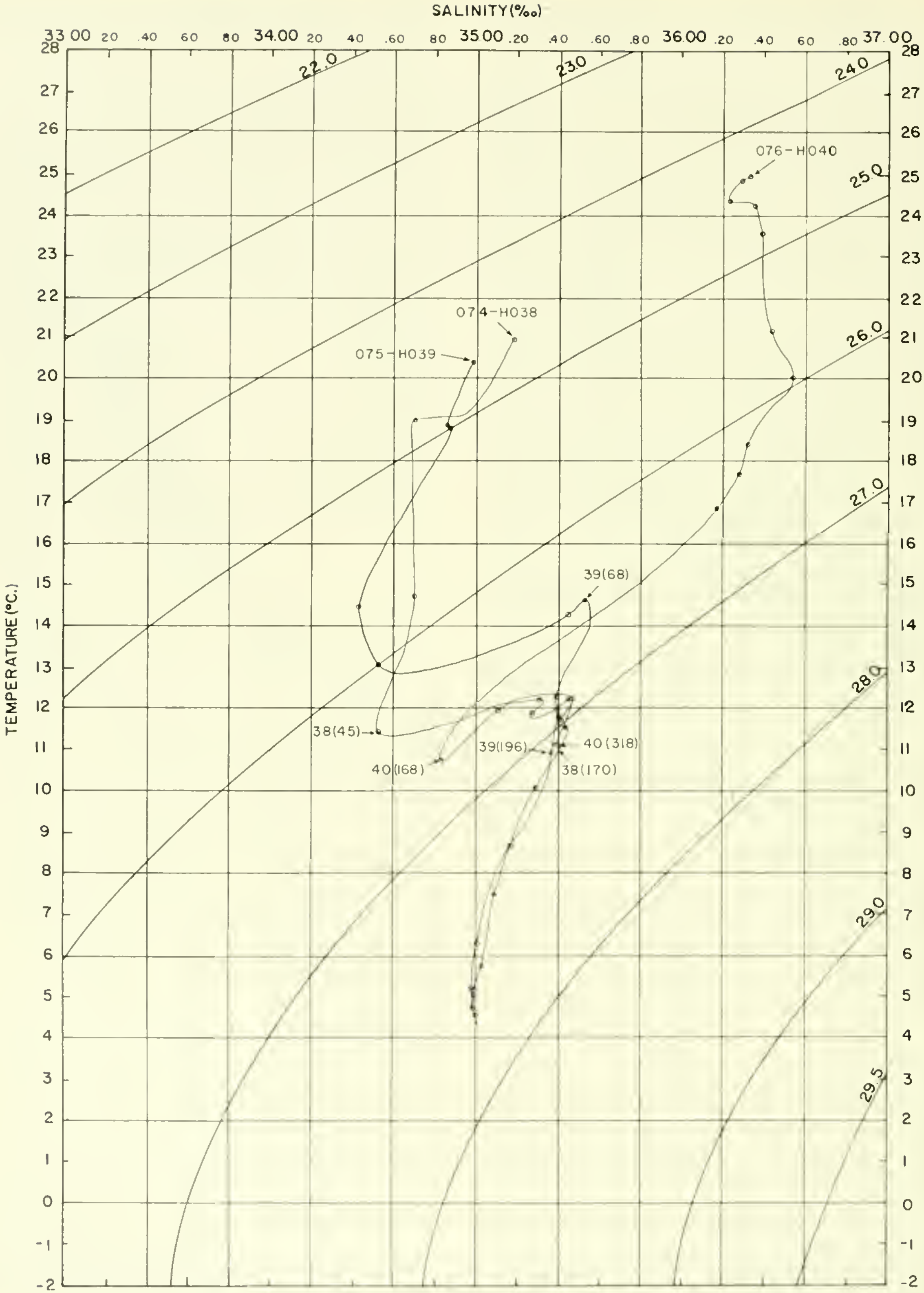


FIGURE 28.—Temperature-salinity curves along section 19. (*See* caption for fig. 27.)

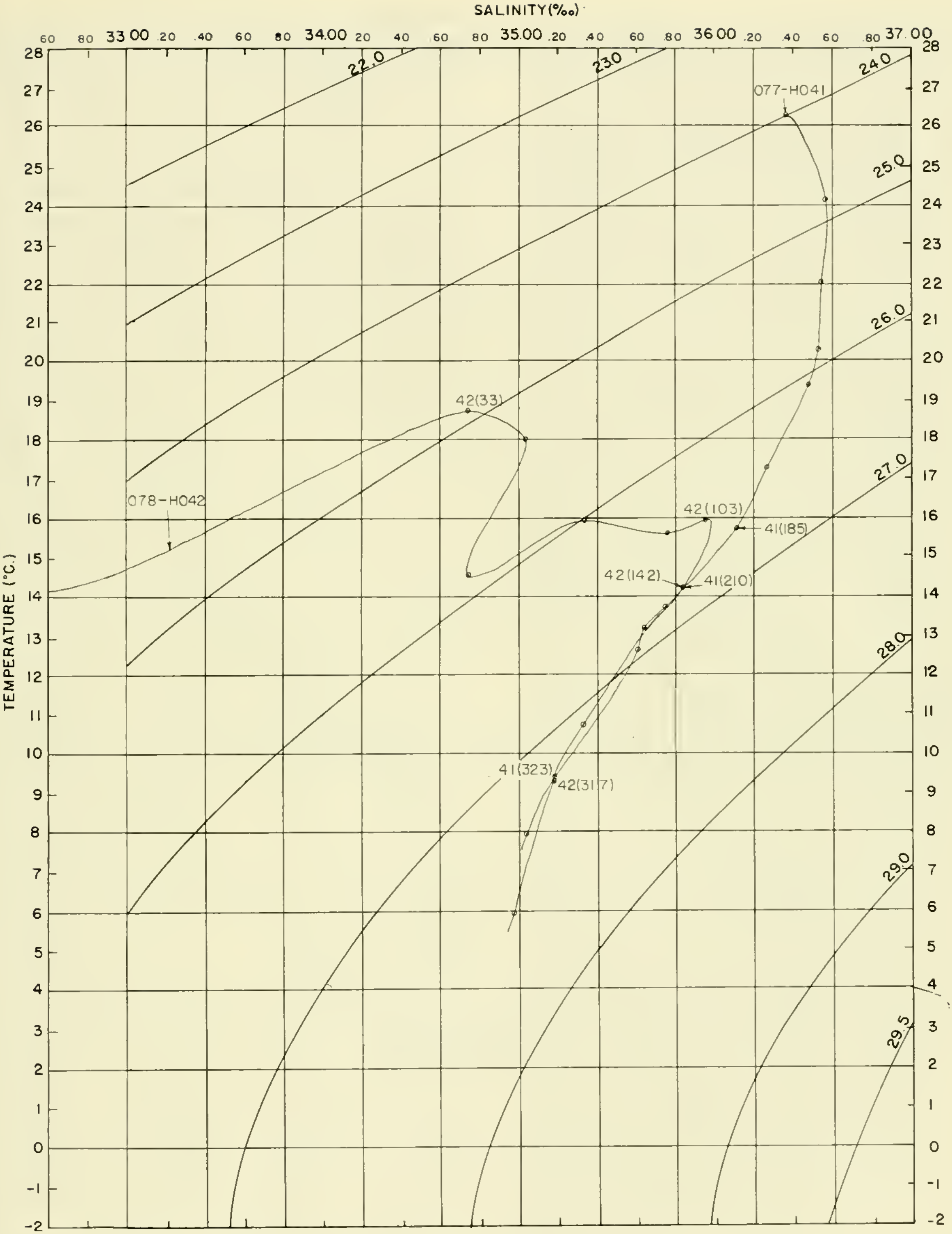


FIGURE 29.—Temperature–salinity curves along section 22. (*See* caption for fig. 27.)

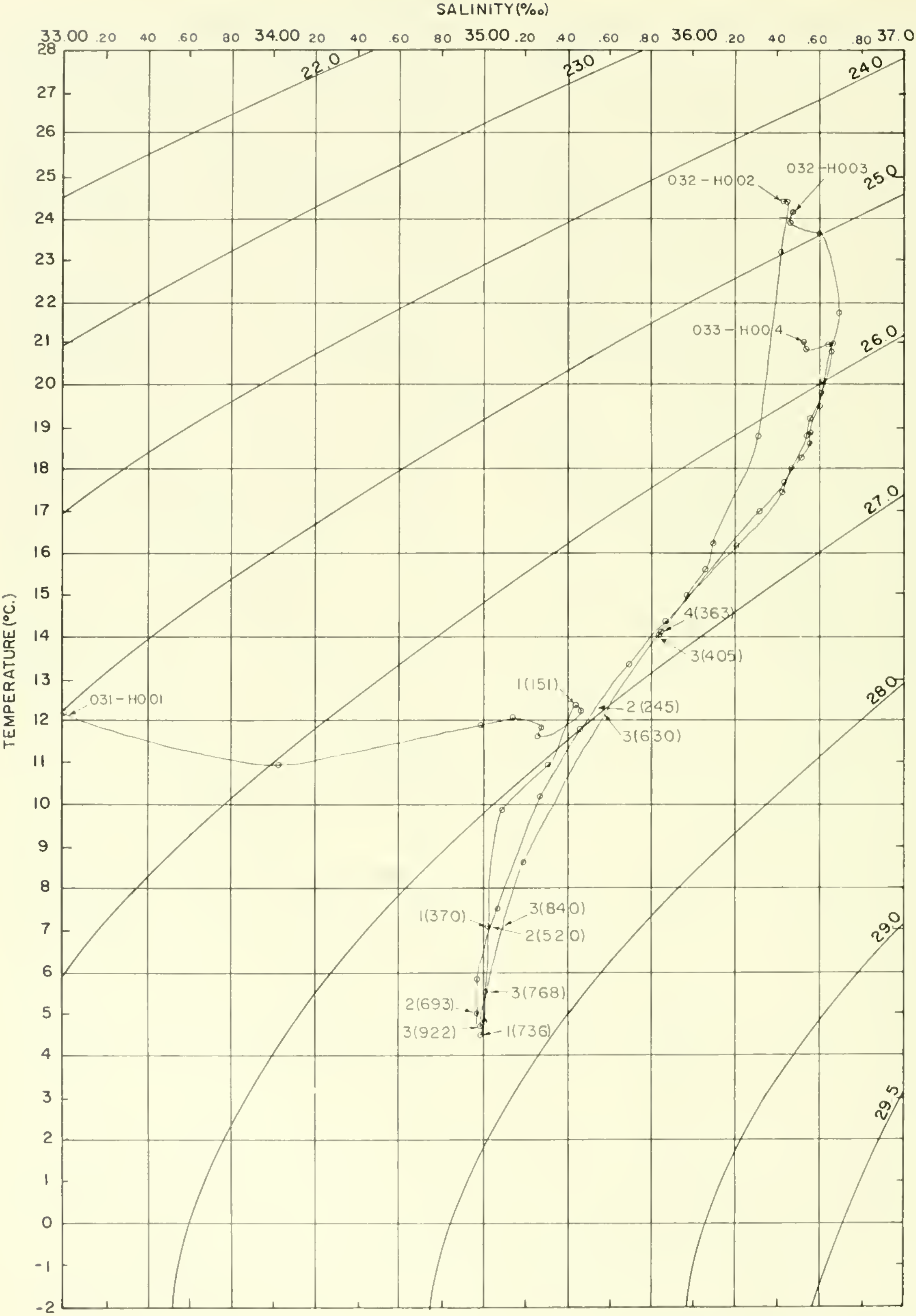


FIGURE 30.—Temperature-salinity curves along section 10. (*See* caption for fig. 27.)

mechanism of mixing during some phase of an interaction cycle, the cross-current component would be produced as a chain effect, and the tendency toward divergence might consequently result in an effective upwelling.

ORIGIN OF THE COLD STRIPES

The cold stripes at the left side of the Gulf Stream are of Shelf water origin, as shown by Ford, Longard, and Banks (1952). Their conclusions were based mainly on two sections (at about long. 55° and 57°) of "Operation Cabot" (1950), which extended over strongly meandering parts of the Gulf Stream. Stommel (1958), generalizing on their results, concluded that the influx of Shelf water must occur somewhere near Cape Hatteras, that the integrity of the cold stripe is maintained for 1,600 miles (2,963 km.), and that water exchange across the boundary is, therefore, negligible.

No such integrity of the cold stripe could be observed during the *Geronimo* cruise. Clear indications that local generation of cold stripes was caused by ascent of cool water may be seen in sections 4 to 7 (figs. 6 to 9). A rather simple boundary structure and no significant cold stripe appear in section 4 (fig. 6). About 12 hours later, when section 6 (fig. 8) was made, the boundary seen in figure 6 was at the same location, but a new boundary and cold stripe were developing strongly 25 miles to the right, far into the Gulf Stream.

The outcropping of cool water seems to have reached a maximum in section 7 (fig. 9). The old boundary is disintegrating below the surface, and the major zone of steeply sloping isotherms is located at the new boundary.

When interaction systems were fully developed and separated from the Gulf Stream by a cold stripe (figs. 10, 14, 16, 17, and 22), the presence of a well-developed mixed layer on both sides of (but not *in*) the stripe, indicated a strong ascending process. Furthermore, the temperatures and salinities of the cold stripes were similar to those in deeper water. For example, the surface temperature in the cold stripe in figure 9 (section 7) is 18° C. No surface salinity values are available for this part of the section, but the previous section (fig. 8) shows a surface salinity of 36.04 ‰ in the newly forming cold stripe (BT 65), while considerably higher surface salinities occur on either side. Salinities and temperatures similar to those found at the surface in the cold stripe in sections 6 and 7 (figs. 8 and 9) were found at a depth of about 160 m. in section 10 at oceanographic station 032–HO02 (fig. 13)—about 20 miles right of the boundary where the isotherms slope steeply. A similar example is provided by the surface conditions at the BT number 269 in figure 17. In figure 22, the surface salinity near the cold stripe (BT 375) is similar to the salinity of the Gulf Stream at 210 m. (station 076–HO40). The hypothesis that the cold stripes were caused by upwelling of water from the area of steeply sloping isotherms seems to be in agreement with the positions of the frontal outcrop as observed from an airplane (Von Arx, Bumpus, and Richardson, 1955). As previously pointed out, a supply of cold, low-salinity water by injection (cold tongues) was also observed during the *Geronimo* cruise. In some portions of the Gulf Stream, this source of cold water to the left of the Gulf Stream may be predominant.

PHOSPHATE DISTRIBUTION

In general, phosphate values were considerably higher in the surface waters of the interaction systems than in the Gulf Stream. Also, phosphate values fluctuated in the interaction systems, associated with interchanging tongues of cold and warm water, and the observed cold-water masses usually showed higher phosphate values. The higher phosphate content of interaction systems could come from various sources, including—although the evidence is sparse— the ascending water. To illustrate this assumption, the only oceanographic station close enough to the cold stripe to be indicative (station 055–HO23 in fig. 17) shows high phosphate values from the surface to about 130 m., low values from about 130 to 300 m., and high values again below 300 m. It seems that at this particular station, ascending water was present above 130 m., and descending mixed water (exhausted of phosphate) between 130 and 300 m. At station 056–HO24 (fig. 17) the phosphate content of the 15° C. water along the steeply sloping isotherms at about 220 m. was about the same. Water in the cold stripe was evidently ascending obliquely at this station, following the sloping density surfaces like Neumann's (1952) "gliding Austausch."

MIXING VOLUMES

According to the described process, Gulf Stream water moves through the interaction system from the surface layer to deeper levels after attaining higher density through mixing. This hypothesis requires mixing of a substantial amount of slope water into the returning mass. Along transect I, the ratio of Gulf Stream water to slope water in the mixture was obtained by applying salinities to the mixing equation, $S(M_1+M_2) = M_1S_1+M_2S_2$ where: M_1 is the mass in the slope water that corresponds to a mean salinity (S_1) of 34.85 ‰. As determined from samples in the upper 150 m., M_2 is the mass of Gulf Stream water corresponding to a mean salinity (S_2) of 36.45 ‰ in the upper 150 m.; S is the resulting salinity of 35.55 ‰, as obtained by computing the mean value of all available T–S curves at the highest points of coinciding properties. The computed proportion of masses was $M_1 = 1.29\ M_2$, which indicates that a somewhat larger amount of slope water than Gulf Stream was supplied to the mixing process. If all mass separated from the Gulf Stream were to return after mixing, the volume of water returning would be more than double, but such total return seems unlikely.

EFFECT ON ENERGY IN THE GULF STREAM

The departure of part of the dense water to the left side of the Gulf Stream below 300 m. would help to maintain the upper 1,000 m. of the water column at a higher density than would otherwise be the case, and the total mass of dense water would also be increased. In addition, the inflow of dense water at the left side of the Gulf Stream should displace lighter water to the right and consequently increase horizontal pressure gradient across the Stream. Thus, a rotation of mass to the interaction system and back to the Gulf Stream would constitute an energy source contributing to the maintenance, and even intensification, of the Stream. It is hardly possible to assess what proportion of the total complex of individual driving and impeding forces of the Stream such a source of energy would represent; too little is known about that complex. It could be expected, however, that the proportion, although unknown, would be greatest in the late winter and spring, when temperature and density differences between Gulf Stream water and inshore water are large.

SUMMARY

Repeated sections along three transects of the Gulf Stream off Chesapeake Bay in the spring of 1963 revealed a process of interaction between the left flank of the Gulf Stream and the adjacent slope water. The data, though incomplete, suggest the following interpretation of the process:

1. Warm, saline water from the left side of the Gulf Stream was shifted to the left by transient intensified convergence in the slope water–Gulf Stream boundary.
2. This warm water became isolated from the Gulf Stream by divergence near the surface and by upwelling.
3. Intense mixing of the separated Gulf Stream water with the slope water generated a dense water type at depths of about 80 to 180 m.
4. Because of the transient occurrences of unstable mass distribution, a part of the water ($\sigma_t > -27.0$) moved downward and along equal density surfaces and joined with the left side of the Gulf Stream at depths of about 250 to 700 m. Some of the mixed water was probably discharged into secondary streams farther downstream and to the left of the main body of the Gulf Stream.

ACKNOWLEDGMENTS

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INTERACTION OF FOOD LEVEL AND EXPLOITATION IN EXPERIMENTAL FISH POPULATIONS

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ABSTRACT

Nine populations of guppies (*Lebistes reticulatus*) were established in separate aquariums. Food supply was constant for groups of three populations in ratios of 0.5, 1.0, and 1.5 to a "standard" diet. Temperature, light, and space were constant and the same for all populations. After 28 weeks, populations had reached near-asymptotic levels, and mean numbers and weights for each group of three were in the same rank as their food levels.

Twenty-five percent, 33 percent, and 50 percent of the fish were removed per 3-week brood interval for each food-level group of three populations, thus providing nine combinations. Continuation of exploitation at these rates led to relatively stable yields during weeks 59 to 72, after initial declines due to readjustment of populations. Yield curves for each food level revealed relation of yield to exploitation rate and biomass to be independent of amount of food consumed. Maximum yields occurred near the 0.33 (33 percent) exploitation rate for all food levels and represented about 25 percent of the food consumed. Results suggest that if commercially fished populations behave as the experimental ones did, management strategies may be applied independently of amount of food organisms available.

The purposes of laboratory fish-population experiments and their relation to other work in fishery dynamics have been set forth rather fully by Silliman (1948) and Silliman and Gutsell (1958). Briefly, the purposes are to provide experimental measurement of the effect of exploitation on stocks of fish, under as fully controlled environmental conditions as possible. The above authors also pointed out the advantages of the guppy (*Lebistes reticulatus*) as an experimental animal: rapid growth and reproductive rates, small size, and hardiness.

Food supply and exploitation rate must be among the most important factors that determine biomass and yield in exploited fish populations. The response of populations to exploitation is well known, as set forth in such works as Beverton and Holt (1957). The importance of food supply, although not as fully documented, is well recognized. For example, Zheltenkova (1961) adduced data indicating that a decreased supply of food reduced the rate of growth and catches of bream in the Sea of Azov. She also reported a number of qualitative examples in another work (1958) that, although lacking numerical estimates of food amounts, tended to support the thesis that food supply is important in determining yield and rate of growth of several fishes in the U.S.S.R. These examples indicate not only the importance of food level at any given time but also the importance of the great fluctuations in this level that occur from one time to another.

Quantitative support for the idea that fluctuations in food supply would modify fluctuations in fish stocks resulting from other causes was provided early by Jensen (1928). His data on measured amounts of bottom food in certain Danish waters in the fall were significantly correlated with catches of plaice.

Because yield is related to both food supply and rate of exploitation, the interaction of these two is of obvious interest to the fishery manager. Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low? The experiments described in this report were

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carried out to throw light on this and similar questions, such as precisely how yields are related to exploitation at each food level. Answers were sought by investigating the effects at controlled exploitation and food level on population biomass and yield.

PLAN OF THE EXPERIMENT

Experimental tanks provided for three food levels and three rates of exploitation, a total of nine combinations. Because of limited facilities and personnel, replications were not made. The experience of Silliman and Gutsell (1958) helped to determine the specific food levels and exploitation rates to use. In each test the levels were chosen to bracket the ones that had provided the greatest yield in the previous experiments. Maximum yield for those experiments occurred when the populations were fed a standard diet and when 25 to 50 percent of the fishable stock was removed per 3-week period (the average interval between broods of a female guppy).

For the experiments reported here, food levels of 0.5, 1.0, and 1.5 times the "standard" diet were arbitrarily selected. An arbitrary selection of exploitation rates at 0.25, 0.33, and 0.50 per 3-week period was also made. The resulting nine combinations were assigned by lot to a row of nine experimental tanks, as follows: Tank A, diet 1.0, exploitation rate 0.25; B, 0.5, 0.25; C, 1.5, 0.50; D, 1.0, 0.50; E, 1.5, 0.25; F, 0.5, 0.33; G, 1.0, 0.33; H, 0.5, 0.50; I, 1.5, 0.33.

The plan of the experiment was simple: To start a population of guppies in each tank and allow all to grow until asymptotic size or a close approach to it had been attained. The populations were then exploited at the chosen rates, and this was continued until the yield from each tank became reasonably stable.

MATERIALS AND METHODS

The experiments were conducted from January 30, 1964, through June 17, 1965, at the former Biological Laboratory, Bureau of Commercial Fisheries, Washington, D.C.

FISH TANKS AND EQUIPMENT

Conventional glass-walled aquariums were used as experimental tanks (fig. 1). The water surface in each was 44 by 24 cm.; and the depth, 19 cm. (volume, 20 l.). Each was provided with a cotton-charcoal filter (inside the tank) and an airstone. A pair of small pumps supplied air for both of these fixtures.

The available room illumination was used as a light source. It consisted of two banks of eight 40-watt fluorescent lamps (fig. 1). (Evidence to be presented later in the section "Changes During Exploitation" will support the assumption that differences in amounts of light received by different populations did not confound the interpretation of the experimental results.) All windows were covered, and lights were controlled by a time switch to be on each day from 6 a.m. to 6 p.m.

Refuges for the young fish were provided by fences placed in the left "front" (facing row of tanks with A to I from left to right as in fig. 1) corners of all tanks. Each fence consisted of glass rods supported by plastic rails. The rods were 21 cm. long and were placed vertically to form a fence 15 cm. long. The center of each glass rod (3 mm. in diameter) was 4.5 mm. from the center of the next rod, leaving spaces of 1.5 mm. between rods for the passage of the young fish. Fences were placed in tanks so as to enclose a 45° right triangular space in the corner of each.

A grader for separation of "fry" from "immature" sizes of fish consisted of a plastic box 20 cm. long with ends 10 cm. square. This box was open at the top, and the bottom was composed of plastic rods, 3 mm. in diameter, placed parallel to the longer axis of the box. Because centers of the rods were 5 mm. apart, 2-mm. spaces were left for grading the fish. All fish which would pass through the grader were classified as "fry"; immature fish which would not were classified as "immature."

EXPERIMENTAL DIET AND PROCEDURES

The diet I used was a standard one developed during previous experiments (Silliman and Gutsell, 1958). Food consisted of medium-grade dry tropical fish food, frozen *Daphnia*, and newly hatched *Artemia* nauplii. The dry food was a commercial product containing dried mosquito larvae, dried flies, dried *Daphnia*, fish-liver meal, beef meal, shrimp meal, salmon-egg meal, wheat-germ meal, fish-roe meal, clam meal, fish-bone meal, dried egg yolk, whole wheat meal, dehydrated kelp, dehydrated alfalfa-leaf meal, dehy-

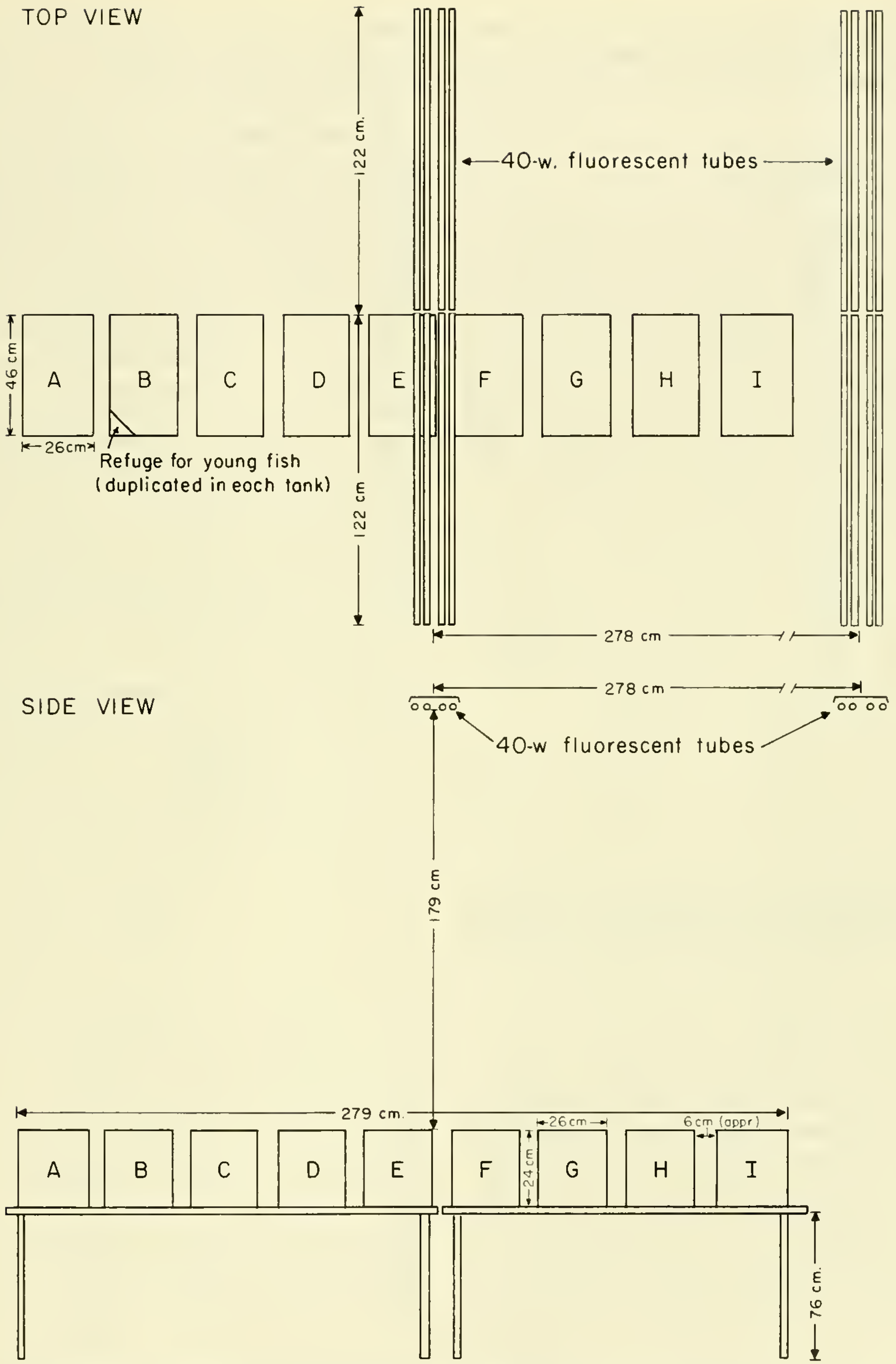
TOP VIEW
122 cm.
40-w. fluorescent tubes
46 cm
26cm
A
B
C
D
E
F
G
H
I
Refuge for young fish (duplicated in each tank)
122 cm
278 cm
SIDE VIEW
278 cm
40-w fluorescent tubes
179 cm
279 cm.
26 cm
6 cm (appr)
24 cm
A
B
C
D
E
F
G
H
I
76 cm.

FIGURE 1.—General arrangement of tanks and orientation with respect to light fixtures. Door to room was located beyond end of light fixture in upper right corner, and was not visible to fish in tanks.

drated carrot, dehydrated lettuce, dehydrated spinach, and dehydrated water cress.

The following analysis was supplied by the maker:

Crude protein, minimum	40 percent
Crude fat, minimum	3 percent
Crude fibre, maximum	10 percent

Artemia nauplii were produced by placing the dry eggs in 750 ml. of salt water (one level tablespoonful per 750 ml.) and incubating them 2 days at about 24° C. Food was supplied to tanks according to the schedule in table 1. All of the daily food allotment was placed in the tanks at one time. During the early part of the experiment some food fell to the bottom of the tanks uneaten; it was siphoned out before the following day's feeding. When the populations had grown to pre-exploitation sizes, all food was consumed.

TABLE 1.—*Schedule of food supplied to tanks receiving various diets. The "standard" diet is designated 1.0*

Day of week	0.5 diet			1.0 diet			1.5 diet		
	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
Sun.			0.05			0.10			0.15
Mon	0.5	0.2	.05	1.0	0.4	.10	1.5	0.6	.15
Tues	.5	.2	.05	1.0	4	.10	1.5	.6	.15
Weds.	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Thurs	.5	.2	.05	1.0	4	.10	1.5	.6	.15
Fri	.5	.2	.05	1.0	4	10	1.5	.6	.15
Sat		.2	.05		.4	10		.6	.15
Total	2.5	1.2	.35	5.0	2.4	70	7.5	3.6	1.05

[1] This represents weight of eggs hatched. Actual weight of nauplii produced, for the "standard" diet was 0.125 mg. (Silliman and Gutsell, 1958). The determination was made by producing duplicate hatches of 0.4 g. of eggs; these hatches were then dried, weighed, and the average weight determined. No data were available to adjust for day-to-day variations in hatching success. The weight of nauplii represented such a small part of the total diet (about 1/100 of 1 percent) that variations would not significantly affect total food available.

The nine populations were started on January 30, 1964. (A list of dates for the numbered weeks of each experiment is given in table 2.) Stocks were from previously established aquariums and consisted of 432 guppies. I segregated the fish into males, females, and "juveniles," the latter including the categories "fry" and "immature" as defined above. All males were placed in a single container and then put into the nine tanks from A to I in succession, one fish at a time. I repeated this process until seven males were in each tank. I used a like process to put eight females in each tank. Similarly, 33 juveniles were placed in each tank, but they were introduced in groups of 10, 10, 10, and 3. Thus, each tank contained 48 fish—7 males, 8 females, and 33 juveniles—chosen in a consistent manner from established aquarium stocks.

Populations were fished (exploited) at 3-week intervals, the approximate time between broods.[1] These rates bracketed the rate previously found to produce maximum yield (Silliman and Gutsell, 1958), which was about 0.33 per 3-week period. The "bracketing" rates were 0.25 and 0.50 per 3-week period. Fishing was done by removing each nth fish for fishing rate $\frac{1}{n}$ and was applied only to the "immature" and "adult" fish, excluding the "fry." "Adults" included all fish whose sex could be determined by external inspection; and "immatures", all others except the "fry" that passed through the grader described above.

Procedures were described in more detail by Silliman and Gutsell (1958), who also reported the technique of weekly counting and weighing the fish. This essentially consisted of counting fish individually and placing them on a strainer. From the strainer fish were transferred to a previously weighed container of water on a balance.

TABLE 2.—*List of calendar weeks included in experiment*

Week No.	Beginning: Year, month, and day	Week No.	Beginning: Year, month, and day
0	*1964* Jan. 26	37	*1964* Oct. 11
1	Feb. 2	38	18
2	9	39	25
3	16	40	Nov. 1
4	23	41	8
5	Mar. 1	42	15
6	8	43	22
7	15	44	29
8	22	45	Dec. 6
9	29	46	13
10	Apr. 5	47	20
11	12	48	27
12	19		
13	26	49	*1965* Jan. 3
14	May 3	50	10
15	10	51	17
16	17	52	24
17	24	53	31
18	31	54	Feb. 7
19	June 7	55	14
20	14	56	21
21	21	57	28
22	28	58	Mar. 7
23	July 5	59	14
24	12	60	21
25	19	61	28
26	26	62	Apr. 4
27	Aug. 2	63	11
28	9	64	18
29	16	65	25
30	23	66	May 2
31	30	67	9
32	Sept. 6	68	16
33	13	69	23
34	20	70	30
35	27	71	June 6
36	Oct. 4	72	13

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[1] Each brood consists of 6 to 60 young, depending on the size of the female (Innes, 1945).

Total weight of fish, container, and water was determined, and the fish weight obtained by subtraction.

ENVIRONMENTAL CONDITIONS

Although temperature was controlled as closely as possible, there were some variations. These were examined in relation to possible effects on growth or survival. Oxygen determinations were also made, to ascertain if the levels were within those considered adequate for warm-water fishes.

TEMPERATURE

Room air temperature was controlled by a thermostatically regulated window heat pump, which could either heat or cool. Water temperature about 8 cm. below the surface of tanks A, E, and I (fig. 1) was recorded daily at about 8 a.m., noon, and 4 p.m. (Only one reading per day was taken on weekends.) The means indicated reasonably stable temperatures (table 3). No 30-day mean deviated more than 0.7° C. from the grand mean. The means for all three times of day gave some indication that tank A averaged higher than the others, but the greatest excess of A over either E or I was 0.5° C. Likewise, the means for all three tanks indicated that the 4 p.m. reading tended to be lower than the others, but again the greatest departure was 0.5° C. The means of "All 3 by All 3" revealed no consistent trend in temperatures during the experiment. The total range of individual temperature readings during the entire experiment was from 21.1° to 27.2° C.

Table 3.—*Mean temperatures for tanks A, E, and I during three 30-day periods* [1]

Period	Temperature recording time	Mean temperature			
		Tank A	Tank E	Tank I	All 3 tanks
		°C.	*°C.*	*°C.*	*°C.*
Mar. 5–Apr. 21, 1964	8 a.m.	24.4	24.1	24.1	24.2
	Noon	24.5	24.4	24.3	24.4
	4 p.m.	23.9	24.0	24.1	24.0
	All 3 times	24.3	24.2	24.2	24.2
Sept. 16–Nov. 2, 1964	8 a.m.	24.9	24.4	24.6	24.7
	Noon	24.4	24.6	24.5	24.7
	4 p.m.	24.8	24.1	24.3	24.3
	All 3 times	24.8	24.3	24.6	24.6
Apr. 23–June 11, 1965	8 a.m.	24.6	24.3	24.3	24.3
	Noon	24.4	24.1	24.0	24.2
	4 p.m.	23.9	23.8	23.6	23.8
	All 3 times	24.3	24.1	23.9	24.1
All 3 periods	All 3 times				24.3

[1] The period means are based on 30 days in which three daily readings were taken in all three tanks. The period is not based on 30 consecutive days. The days that were excluded from the periods were ones in which fewer than three readings were made (these days usually were on weekends).

The rather small deviations just recorded suggest that temperature was fairly well controlled. Any effects on growth or survival must have been slight, and no further analysis of temperatures seems justified.

OXYGEN CONCENTRATION

Oxygen determinations were made for each tank during March 29 to April 14, 1965. Readings ranged from 4.54 to 5.58 p.p.m., all within or above the 3 to 5 p.p.m. that Lewis (1963) considered adequate for warm-water fishes.

Ozone was used in the tanks to control algae during weeks 56–72. This was supplied by a "Sander Ozonizer" [2] at the rate of 5 mg. per hour. Except for occasional treatments of individual tanks, the 5 mg. per hour was delivered to the main air supply, thus being divided among the nine tanks. Previous tests with fish not included in the experiments produced no mortalities when the entire 5 mg. per hour was supplied to a single 20-l. tank. No relation was noted between growth of algae and food supply or amount of light.

POPULATION CHANGES

For purposes of analysis, the experiment was arbitrarily divided into periods before (weeks 0–28), and after (weeks 29–72) exploitation began. Changes during the first period reflected increases in number and biomass resulting from reproduction and growth. Exploitation was responsible for the major changes in the second period, resulting in initial declines followed by relative stability in both population size and yield.

INITIAL GROWTH OF POPULATIONS

The stocks entered a period of growth in numbers and weight, each stock influenced by the amount of food supplied. Mean numbers and weights each week for the group of three tanks at each food level (tables 4 and 5, and fig. 2) clearly bring out the influence of food supply on growth. Total weights of the stocks were in the same rank as, but not exactly proportional to, amounts of food supplied. During weeks 21 to 28, mean weights for diet levels 0.5, 1.0, and 1.5 were 14.5, 26.0, and 36.6, respectively. These

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

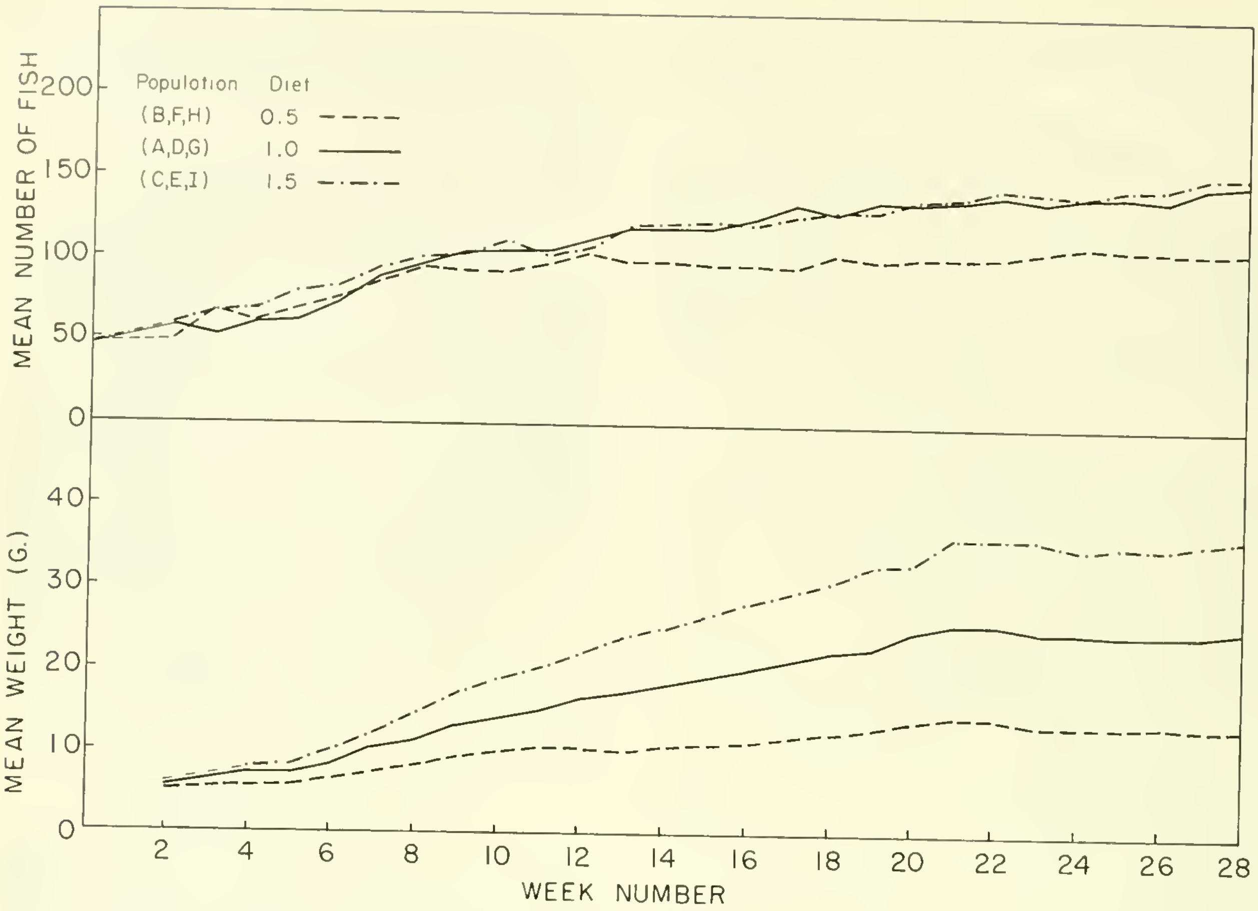

FIGURE 2.—Initial growth of populations. Data are means for the three populations at each diet level.

were in ratios 1.00:1.79:2.52 as compared with the 1:2:3 ratios of the diet levels.

Average numbers of fish fell even farther from the ratios of the diet levels than did the average weights. For weeks 21 to 28 they were 110, 145, and 149 in ratios 1.00:1.32:1.35. Comparison of these ratios with those for average weights indicated that the individual fish averaged larger at the higher diet levels. Weights of individual fish averaged 0.132, 0.179, and 0.246 g., respectively, in populations at diet levels 0.5, 1.0, and 1.5.

These results indicate that the greater biomass at the higher diet levels than at the lowest level was caused by both better survival and more rapid growth of individuals. Growth was the more important factor. The results indicate also somewhat less efficient food use at the higher diet levels than at the lowest, in the sense of the amount of biomass supported by a given amount of food. Thus, the 2.85 g. of food consumed per week (totals for *Daphnia* and dry food from table 1, plus 6 times ½ of 0.000125 g. for *Artemia*), at the 0.5 diet level supported a biomass of 14.5 g., or 5.1 g. per gram of weekly consumption, whereas at the 1.5 diet level the comparable figures are 8.55 g., 36.6 g., and 4.3 g. This loss of efficiency may have been the result of crowding the larger biomass at the higher diet levels into the same amount of space as occupied by the biomass at the lowest diet level. Alternatively, it is possible that such efficiency may simply be a declining function of size in stabilized populations.

TABLE 4.—*Weekly numbers of fish in each lettered tank during period of initial growth, first 28 weeks*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank II	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
0	48	48	48	48	48	48	48	48	48	48	48	48
1	(1)	(1)	(1)	......	(1)	(1)	(1)	......	(1)	(1)	(1)	......
2	52	54	45	50	60	47	70	59	86	49	46	60
3	89	51	65	68	43	45	72	53	74	62	66	67
4	58	50	74	61	42	71	70	61	79	59	69	69
5	80	53	78	70	50	71	69	63	100	67	73	80
6	90	61	77	76	66	73	84	74	122	73	73	89
7	122	67	77	87	68	110	89	89	122	75	87	95
8	119	93	75	96	76	121	95	97	121	77	105	101
9	121	83	76	93	113	110	92	105	131	79	99	103
10	121	81	77	93	99	111	107	106	145	95	100	113
11	130	82	82	98	95	125	115	112	136	85	105	109
12	142	92	81	105	97	144	116	119	138	85	103	109
13	120	97	82	100	115	134	114	121	171	94	102	122
14	121	95	83	100	110	140	117	122	166	94	111	124
15	124	94	78	99	103	139	120	121	161	95	120	125
16	122	95	80	99	106	154	119	126	160	93	116	123
17	120	89	83	97	119	155	135	136	167	100	121	129
18	129	102	87	106	113	149	130	131	181	99	117	132
19	122	101	83	102	122	151	141	138	183	97	115	132
20	125	105	85	105	125	151	138	138	203	99	117	140
21	124	103	89	105	121	158	141	140	182	104	138	141
22	126	103	88	106	130	165	134	143	191	127	122	147
23	133	109	88	110	125	163	132	140	198	118	119	145
24	135	114	89	113	129	160	144	144	195	116	119	143
25	132	112	88	111	133	159	141	144	198	122	127	149
26	135	112	87	111	131	152	143	142	193	122	135	150
27	131	111	87	110	133	159	160	151	209	123	139	157
28	127	117	88	111	144	160	155	153	207	122	142	157

[1] Not counted.

TABLE 5.—*Weekly weights of fish in each lettered tank and mean weight per diet during period of initial growth, first 28 weeks*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank H	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
0	(1)	(1)	(1)	......	(1)	(1)	(1)	......	(1)	(1)	(1)	......
1	(1)	(1)	(1)	......	(1)	(1)	(1)	......	(1)	(1)	(1)	......
2	5.5	4.6	5.9	5.3	6.5	5.5	5.7	5.9	4.8	7.7	6.1	6.2
3	5.3	5.3	6.5	5.7	7.0	6.6	6.5	6.7	6.3	(3)	(3)	......
4	5.6	5.8	6.5	6.0	8.2	7.1	7.6	7.6	7.8	8.7	7.8	8.1
5	5.3	6.4	6.2	6.0	7.3	7.1	8.8	7.7	9.3	8.3	8.4	8.7
6	6.3	7.6	7.0	7.0	7.8	8.6	10.0	8.8	11.0	10.0	10.3	10.4
7	6.7	8.9	7.7	7.8	9.5	10.5	12.5	10.8	13.5	12.3	12.2	12.7
8	8.3	9.3	8.5	8.7	11.3	11.4	12.0	11.6	16.2	14.5	14.2	15.0
9	8.7	11.0	9.8	9.8	13.0	13.5	13.7	13.4	18.6	17.1	16.4	17.4
10	9.6	10.9	10.4	10.3	13.6	15.0	14.8	14.5	20.0	19.0	18.8	19.3
11	10.0	12.3	10.4	10.9	15.2	16.2	15.8	15.7	21.7	20.5	19.9	20.7
12	10.4	11.2	10.9	10.8	16.6	16.8	17.5	17.0	24.2	22.9	21.0	22.7
13	10.9	10.4	10.9	10.7	17.3	17.6	18.3	17.7	25.8	24.2	22.9	24.3
14	11.4	10.6	11.8	11.3	18.2	18.6	18.9	18.6	26.3	25.8	24.8	25.6
15	12.1	11.4	11.5	11.7	19.4	19.9	19.7	19.7	27.9	27.0	26.6	27.1
16	12.2	11.8	11.8	11.9	20.4	20.4	21.0	20.6	29.7	29.2	27.5	28.8
17	12.6	12.2	12.2	12.3	21.6	21.2	22.3	21.7	31.6	30.2	28.3	30.0
18	13.7	12.8	12.4	13.0	23.0	22.5	23.4	23.0	33.3	31.8	29.2	31.4
19	12.7	13.1	15.2	13.7	22.8	23.2	24.1	23.4	33.8	32.7	33.3	33.3
20	15.6	14.5	14.0	14.7	25.6	24.4	26.4	25.5	35.6	33.6	32.2	33.8
21	17.3	14.2	14.4	15.3	26.0	26.5	27.4	26.6	38.2	39.4	33.3	37.0
22	16.0	14.3	14.9	15.1	26.4	25.8	26.9	26.4	40.5	37.0	33.3	36.9
23	14.6	14.4	13.9	14.3	25.8	24.9	26.3	25.7	40.8	37.6	32.5	37.0
24	14.4	14.2	13.9	14.2	25.5	25.5	26.6	25.9	38.2	35.9	33.0	35.7
25	14.3	14.6	13.7	14.2	25.4	24.4	26.3	25.4	40.0	35.7	32.9	36.2
26	15.2	14.5	14.1	14.6	27.2	(2)	26.6	......	40.1	35.4	32.5	36.0
27	14.2	14.5	13.7	14.1	25.7	24.9	26.9	25.8	39.5	35.8	34.5	36.6
28	14.1	14.7	13.9	14.2	25.2	25.7	27.8	26.2	38.8	35.6	37.7	37.4

[1] Not weighed.
[2] No record.
[3] Aberrant data discarded.

It was desired to have the populations as stable as possible before the start of exploitation. Degree of stability was examined by studying the distribution of the individual populations with respect to the categories "fry," "immature," and "adult." For the 3 weeks immediately before the start of exploitation at each diet level, compositions according to these categories revealed fairly consistent patterns for the 0.5 and 1.0 levels (figs. 3 and 4), both between weeks and between populations. (Weeks of removal were staggered to facilitate the laboratory routine. Thus, exploitation at the 0.5 level began a week after that at the 1.0 level.) The compositions are characteristic of mature populations at or near the asymptotic level—mostly adults that are rather stable in number and much smaller and somewhat more fluctuating numbers of juveniles.

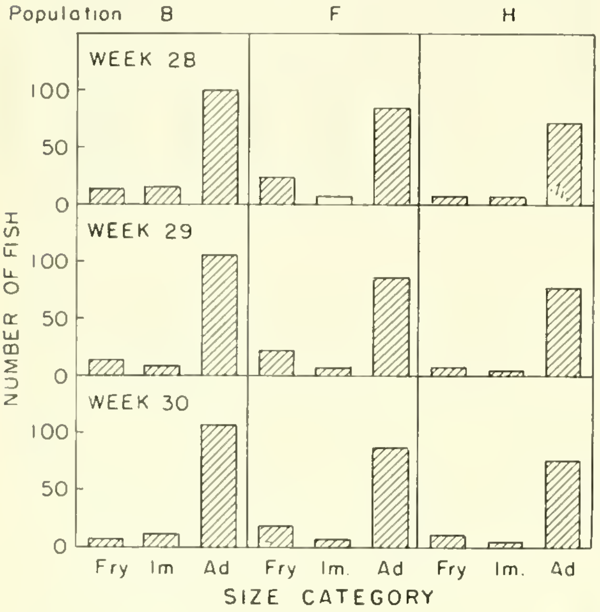

FIGURE 3.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 0.5 diet level, immediately before exploitation.

Characteristics of the compositions were similar at the 1.5 level (fig. 5) except for the lack of consistency between populations. (Exploitation was delayed 4 weeks in the hope that this inconsistency might disappear.) Here the differences are marked both in total number (as between C and E in week 34) and in percentage composition (as between C and I in week 32). These differences are surprising among populations held for more than 30 weeks under conditions of food supply, temperature, light, and space as nearly identical as possible. No ready explanation could be found among other conditions of the environment or among procedures of handling the fish. Probably genetic differences were not averaged out among the rather small numbers of adults (15) in the initial populations, in spite of the method of selection (section, "Initial growth of populations"). The differences may also have resulted from variations in gravidity among the eight adult females in each initial population. Support for some explanation related to the initial populations is found in the fact that C exceeded E and I in number and weight almost from the start of the experiment (weeks 2 to 28, table 3; weeks 5 to 20 and 22 to 28, table 4).

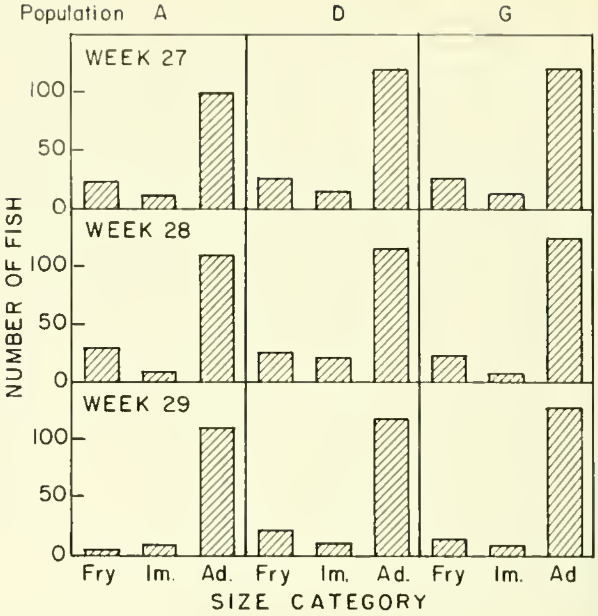

FIGURE 4.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 1.0 diet level, immediately before exploitation.

The differences among populations at the 1.5 diet level persisted, even though the start of exploitation was delayed 4 weeks beyond that for

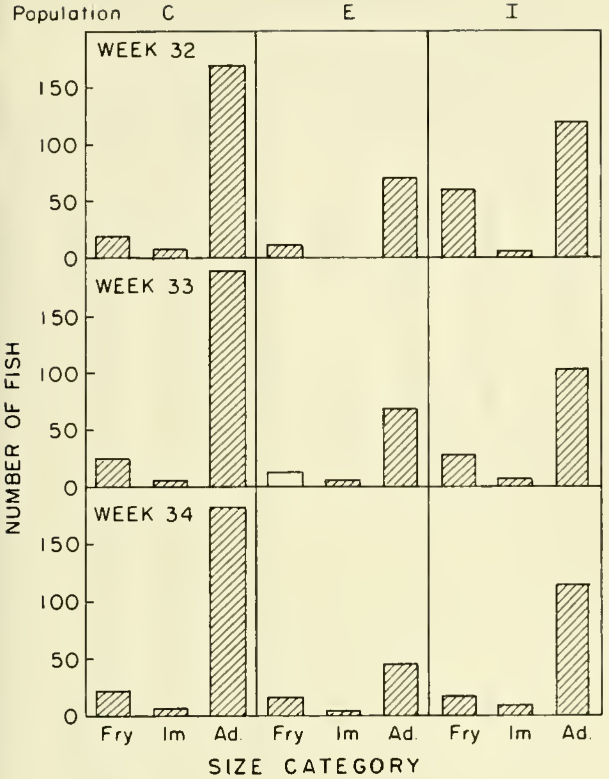

Figure 5.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 1.5 diet level, immediately before exploitation.

the other six populations. I decided to proceed with exploitation of the 1.5 level group because of the substantial amount of time and effort already invested and the desire to have yields comparable with those for the other populations. This decision was supported by the fact that compositions were fairly stable within populations (fig. 5) even though discrepant between them.

Response of the populations to exploitation is indicated by the mean numbers and weights for each diet level (tables 6 to 9 and fig. 6). The saw-tooth pattern of reduction by removals and subsequent recovery is characteristic. As pointed out by Silliman and Gutsell (1958), this kind of variation reflects the resilience of natural populations as long as exploitation rates are not high enough to cause extinction.

As was also mentioned by Silliman and Gutsell, population weights are more stable than population numbers, since the latter are affected more by entrance and mortality of broods of fry. The weights reveal the typical decline in population size after the inception of exploitation, followed by near stability during the final weeks of the experiment. Although populations at all three diet levels decreased in biomass under exploitation, they maintained the preexploitation rank, which was the same as that of the diet levels.

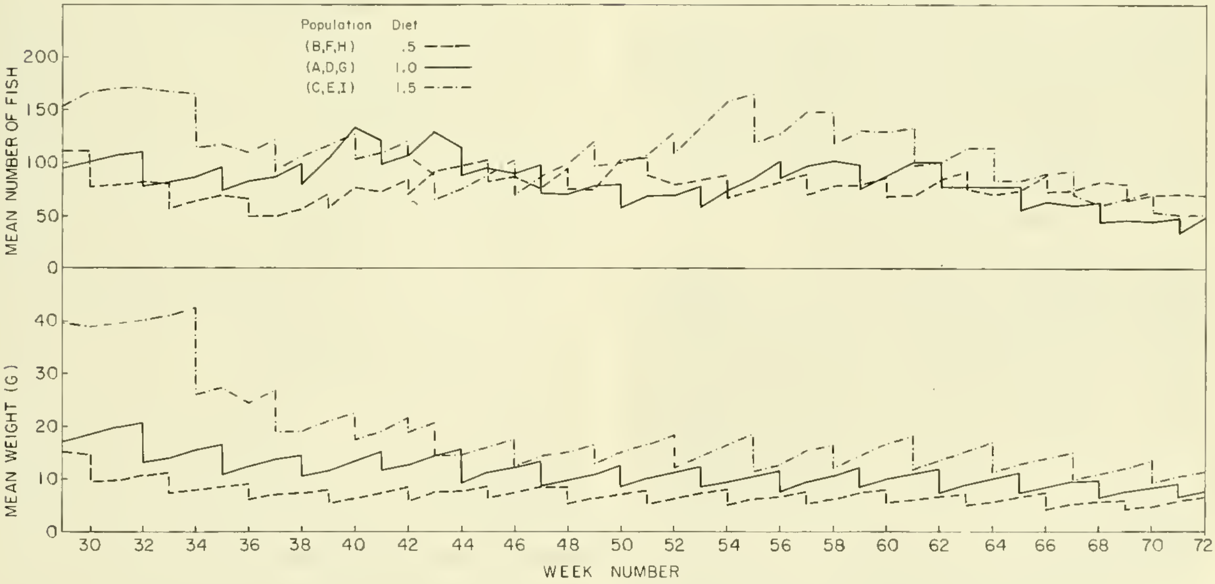

Figure 6.—Response of populations to exploitation. Data are means for each diet level.

Table 6. *Weekly numbers and food-level means for each tank during period of exploitation; postremoval numbers for removal weeks were obtained by subtracting numbers removed (table 7); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet, and week 34 for 1.5 diet*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
29	127	118	91	112	122	158	148	143	204	126	133	154
30	127	114	93	111	104	90	110	101	217	141	141	166
31	101	80	52	78	105	104	110	106	217	143	150	170
32	97	83	67	82	119	93	119	110	200	126	184	170
33	100	87	54	80	96	52	91	80	221	142	138	167
34	90	65	34	63	99	62	93	85	211	158	141	170
35	98	72	36	69	95	71	123	96	131	109	111	117
36	82	69	46	66	73	79	95	82	133	69	124	109
37	70	50	27	49	75	77	106	86	146	74	142	121
38	73	62	34	56	90	74	133	99	107	94	118	106
39	93	72	45	70	107	71	134	104	129	109	111	116
40	82	62	83	76	92	134	172	133	135	122	121	126
41	85	59	72	72	98	131	131	120	114	112	100	109
42	92	97	60	83	82	94	143	106	136	118	106	120
43	106	97	70	91	115	113	157	128	89	97	77	88
44	114	99	71	95	94	101	149	115	68	65	91	75
45	126	110	66	101	80	104	100	95	70	83	112	88
46	107	91	60	86	82	101	85	89	73	92	139	101
47	110	63	51	75	91	108	91	97	77	45	137	86
48	106	122	53	94	69	76	61	69	73	60	160	98
49	87	100	38	75	67	88	75	77	75	112	174	120
50	88	131	85	101	71	89	76	79	39	105	154	99
51	94	135	84	104	101	53	52	69	29	98	193	107
52	71	104	63	79	88	51	67	69	57	130	198	128
53	70	109	69	83	101	50	81	77	76	145	175	132
54	70	125	65	87	109	26	87	74	86	172	220	159
55	63	118	42	74	116	39	101	85	88	159	247	165
56	70	117	55	81	150	52	102	101	106	58	216	127
57	80	121	65	89	148	49	95	97	128	81	234	148
58	74	116	43	78	141	55	107	101	119	78	242	146
59	75	111	47	78	141	56	98	98	108	87	192	129
60	109	105	46	87	139	44	81	88	107	80	196	128
61	90	88	25	68	135	44	122	100	110	95	194	133
62	86	104	62	84	150	49	94	98	63	85	152	100
63	115	107	51	91	120	33	77	77	66	129	148	114
64	97	81	33	70	120	36	74	77	68	126	149	114
65	103	86	33	74	109	31	89	76	39	105	103	82
66	108	88	69	88	88	20	78	62	54	110	102	89
67	97	76	49	74	93	26	60	60	59	112	106	92
68	121	76	49	82	92	28	65	62	32	82	67	60
69	118	74	47	80	68	19	50	46	33	81	85	66
70	118	64	28	70	68	18	47	44	33	94	93	73
71	107	78	29	71	79	21	44	48	20	65	68	51
72	102	74	31	69	77	11	58	49	26	63	66	52

YIELDS

Removals during the period of exploitation were comparable to the catches of commercial fisheries and provided information on stabilized yields. Data were analyzed both to determine when relative stability began and to measure the relation of yield to amount of food consumed.

COMPARATIVE YIELDS

Yields as well as population sizes were more stable in weights than in numbers; therefore, yields were studied in terms of weight. The course of yield for each population during the exploitation period (table 9 and fig. 7) included an initial period of decline as the populations adjusted themselves to removals. This decrease was followed by a period of relative stability beginning about week 49.

Even within the relatively stable period, yields showed considerable irregularity. This phenomenon resulted from variations in the response of the populations to exploitation and from deviations of the percentages removed from the exact nominal exploitation rates. The latter deviations occurred because the removal rates were applied on the basis of numbers of fish rather than weights. Some of this random variability is averaged out in means of yields for three 14- or 15-week subperiods covering the entire period of exploitation (table 9 and fig. 8). These means again reflect the initial period of decline, followed by more stable yields.

The final period, including weeks 59 to 72, was one of fairly stable yield (fig. 7). Mean yields for this period (fig. 8) ranked the same according to exploitation rate for the 1.0 and 1.5 diets. Yields at the 0.5 diet were nearly identical. The period including weeks 59 to 72 fairly well fulfilled the planned objective of "a reasonably stable yield" (section, "Plan of the Experiment"), and data from it were used in the study of relation between food level and exploitation rates. Results from this period had the additional advantage of being

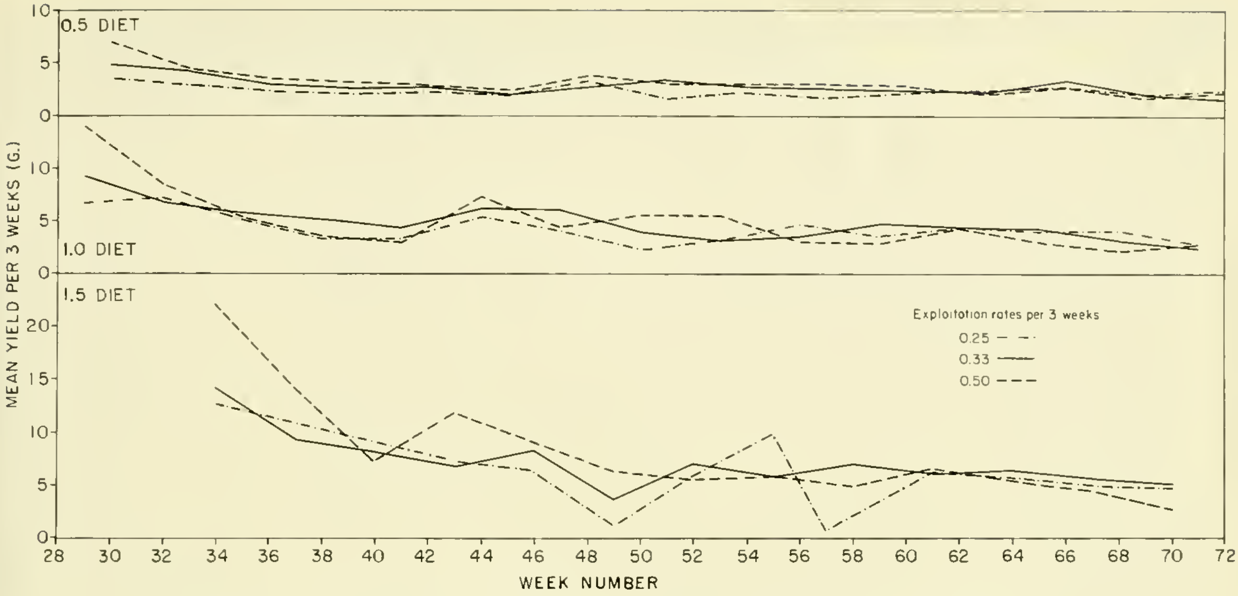

Figure 7.—Yield per three weeks of each population during period of exploitation.

free from the irregularities in removals and mortalities that occurred at the 1.5 diet level during weeks 37 to 57 (table 7, footnotes).

RELATION BETWEEN YIELD AND FOOD LEVEL

Data in the preceding section showed that yields at the 1.0 and 1.5 diets were related to exploitation rate, but that no such relation was detectable at the 0.5 diet. The available data may now be brought together in an attempt to answer such questions as that posed in the introduction: "Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low?" It is instructive here to relate the yields to the average total weight or biomass of the populations (table 10). Because the populations were allowed to reach asymptotic size or a close approach to it, an additional point for each yield-biomass curve is available—that at zero rate of exploitation. If small deviations are charged to random variability, the appropriate curves (fig. 9) reveal a regular relation among exploitation rate, biomass, and yield at each diet level (curves fitted by inspection).

The curves suggested that the relation of yield to exploitation rate tends to be independent of diet level. Absolute yields were obviously dependent on amount of food available, but the greatest yield at each diet level occurred at or

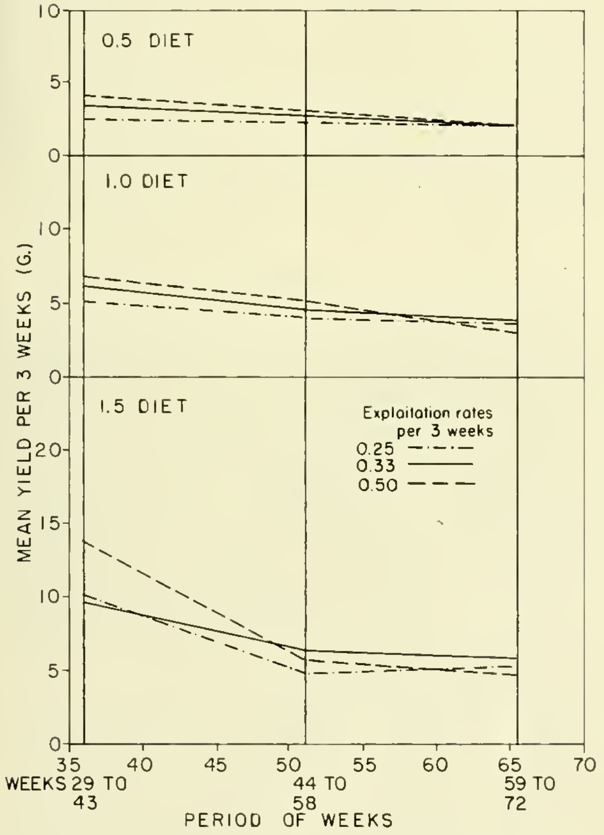

Figure 8.—Mean yields for three 14- or 15-week periods. Location of vertical lines along horizontal scale indicates center of each period.

TABLE 7.—*Numbers removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
29					29	45	68	47				
30	29	31	41	33								
31												
32					23	35	40	33				
33	24	25	23	24								
34									29	43	95	56
35					19	25	24	23				
36	18	16	15	16								
37									[1] 0	30	55	28
38					16	23	24	21				
39	14	14	12	13								
40									[1] 0	30	41	24
41					14	24	27	22				
42	12	13	18	14					0	0	[2] 43	14
43									22	24	24	23
44					18	33	32	28				
45	18	16	26	20								
46									[3] 71	24	[4] 0	32
47					18	28	35	27				
48	15	21	21	19								
49									11	27	36	25
50					15	21	30	22				
51	17	21	15	18								
52									15	35	13	21
53					14	16	24	18				
54	17	20	23	20								
55									[3] 72	43	24	46
56					18	19	12	16				
57	13	24	23	20					[5] 15			
58										46	27	29
59					22	24	23	23				
60	14	23	21	19								
61									19	47	46	37
62					24	24	18	22				
63	14	22	11	16								
64									15	45	33	31
65					24	24	15	21				
66	14	19	17	17								
67									20	31	18	23
68					24	20	7	17				
69	14	18	15	16								
70									20	23	16	20
71					17	13	9	13				
72	15	14	16	15								

[1] Removals omitted because of accidental mortalities in week 36.
[2] Removals by error; added to week 43 removals in subsequent treatment.
[3] Includes accidental mortality.
[4] Omitted because of erroneous removals in week 43.
[5] Accidental mortality considered to replace removals due in week 58.

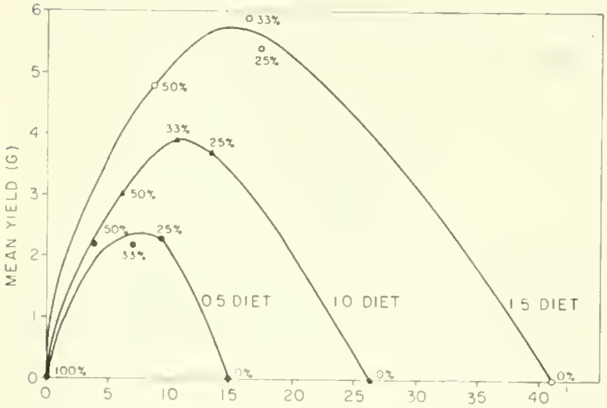

FIGURE 9.—Curves indicating relation of yield per 3-week brood interval to biomass and exploitation rate (indicated percentages) at each diet level. Points indicated for 0 percent exploitation rate are average population levels for the 3 weeks immediately before exploitation.

near the 0.33 exploitation rate (assuming that the different exploitation-yield relation at the 0.5 diet was due to random variation rather than a real difference in the relation). If the apparent independence of the exploitation-yield relation from food level reflects what happens in commercially fished populations, the finding is significant to fishery administration. Such independence would mean that the same management strategy might be applied when food organisms are scarce as when they are abundant.

From the viewpoint of the commercial fisherman, an exploited population is a machine for converting aquatic food to marketable fish flesh. It is of interest to see how efficiently our model of the machine operated at each food level. Maxima of the yield curves (fig. 9) indicate yields per 3 weeks of about 2.4, 3.9, and 5.8 g. at the 0.5, 1.0,

TABLE 8.—*Weekly weights and food-level means for each tank during period of exploitation; postremoval weights for removal weeks were obtained by subtracting weights removed (table 9); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet and week 34 for 1.5 diet*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank II (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
29	14.2	15.3	17.5	15.7	26.1	26.8	28.4	27.1	45.2	37.5	35.9	39.5
30	14.6	15.5	14.7	14.9	19.9	14.9	20.2	18.3	42.2	38.1	37.4	39.2
31	11.5	10.1	8.2	9.9	21.0	16.9	21.5	19.8	(1)	41.0	37.6	------
32	11.9	11.3	8.9	10.7	22.0	17.4	22.6	20.7	42.2	39.5	39.0	40.2
33	12.1	12.0	9.4	11.2	15.6	10.1	16.6	14.1	43.7	40.8	38.6	41.0
34	9.6	8.3	5.9	7.9	17.2	11.7	18.0	15.6	45.7	42.7	39.1	42.5
35	10.3	9.0	6.8	8.7	17.6	13.2	19.2	16.7	23.6	30.8	27.7	27.4
36	10.9	9.4	7.3	9.2	14.0	9.0	14.8	12.6	25.8	19.8	28.4	24.7
37	8.7	8.1	4.9	7.2	15.3	10.1	16.0	13.8	30.0	20.5	30.6	27.0
38	9.4	7.9	5.1	7.5	15.8	11.3	17.0	14.7	14.3	21.5	21.9	19.2
39	9.7	8.5	6.1	8.1	12.8	9.2	13.2	11.7	16.3	23.4	23.4	21.0
40	7.8	7.0	4.5	6.4	14.2	11.0	14.7	13.3	17.2	25.4	25.4	22.7
41	8.7	7.8	5.5	7.3	16.0	12.6	16.7	15.1	12.6	26.0	19.0	19.2
42	10.2	8.6	6.8	8.5	13.8	10.5	14.5	12.9	15.7	28.3	21.3	21.8
43	8.6	7.1	7.2	7.6	15.3	12.5	15.2	14.3	9.5	30.4	22.4	20.8
44	8.6	8.2	6.5	7.8	16.5	13.8	16.8	15.7	7.5	17.1	18.7	14.4
45	10.1	9.3	7.2	8.9	12.9	8.6	12.2	11.2	9.6	18.5	20.2	16.1
46	9.1	8.2	6.1	7.8	13.6	9.6	13.7	12.3	12.2	19.8	21.3	17.8
47	9.8	9.3	6.6	8.6	15.0	11.6	14.3	13.6	14.2	14.1	15.0	14.4
48	10.1	9.1	7.1	8.8	11.6	8.3	9.8	9.9	14.6	14.6	16.1	15.1
49	7.6	7.3	4.2	6.4	12.5	9.0	11.2	10.9	16.2	15.7	18.2	16.7
50	8.5	8.1	5.3	7.3	14.0	10.7	13.0	12.6	12.2	16.9	16.6	15.2
51	9.3	9.3	5.6	8.1	13.3	6.8	10.3	10.1	11.3	19.0	19.5	16.6
52	8.4	6.9	3.7	6.3	14.0	8.0	11.5	11.2	12.5	21.3	21.5	18.4
53	9.0	7.9	4.6	7.2	15.8	9.2	12.8	12.6	8.5	17.7	17.1	14.4
54	9.7	8.8	5.7	8.1	12.2	4.8	11.1	9.4	10.2	19.6	19.6	16.5
55	7.9	6.9	4.3	6.4	13.2	5.9	12.9	10.7	12.3	22.3	21.6	18.7
56	8.5	7.5	4.4	6.8	15.2	6.6	13.6	11.8	7.5	13.5	17.3	12.8
57	9.4	8.4	5.9	7.9	12.2	5.0	11.3	9.5	9.6	16.0	20.6	15.4
58	8.6	6.9	3.6	6.4	13.1	6.4	12.0	10.5	11.3	16.1	22.0	16.5
59	10.3	7.9	4.7	7.6	14.9	7.7	14.3	12.3	8.4	18.0	16.6	14.3
60	10.8	8.1	5.6	8.2	13.1	6.5	10.6	10.1	10.9	20.0	18.9	16.6
61	9.2	6.5	3.6	6.4	14.7	7.6	11.7	11.3	12.6	21.6	20.7	18.3
62	9.5	7.2	4.4	7.0	15.8	8.5	12.1	12.1	8.2	17.5	16.3	14.0
63	10.3	7.9	4.3	7.5	12.1	5.5	9.6	9.1	10.6	18.3	16.6	15.2
64	8.8	6.4	2.9	6.0	13.5	6.7	10.7	10.3	12.3	19.5	20.1	17.3
65	9.6	7.5	3.8	7.0	14.5	8.2	11.2	11.3	8.6	15.6	14.7	13.0
66	10.3	8.0	4.5	7.6	11.6	5.7	8.6	8.6	8.4	17.3	16.5	14.1
67	8.2	6.0	2.6	5.6	13.0	6.4	10.0	9.8	9.5	18.2	18.0	15.2
68	8.8	6.2	3.2	6.1	13.7	6.0	10.9	10.2	5.6	14.8	13.5	11.3
69	8.8	7.0	3.8	6.5	11.6	4.3	8.2	8.0	6.6	16.0	14.6	12.4
70	7.8	5.5	2.5	5.3	12.5	4.9	8.8	8.7	8.0	18.3	15.7	14.0
71	8.2	6.6	4.0	6.3	13.1	5.3	10.4	9.6	5.9	14.6	12.6	11.0
72	9.7	6.9	4.6	7.1	11.6	3.1	9.2	8.0	6.4	15.7	13.6	11.9

[1] Aberrant datum discarded.

and 1.5 diet levels, respectively. Amounts of food consumed at these levels were 8.55, 17.10, and 25.65 g. per 3 weeks (sum of weekly totals for *Daphnia* and dry food plus 6 [0.000125 × diet ratio] for *Artemia*, all multiplied by 3, table 1); thus, conversion efficiencies were 0.28, 0.23, and 0.23. Again, the small difference at the 0.5 diet level probably is not significant. For practical purposes the conversions at all three diet levels are identical and are close to the 0.20 reported by Silliman and Gutsell (1958).

I conclude that efficiency of food conversion, as well as relation between exploitation rate and yield, is independent of amount of food available for the laboratory populations within the range of observation. Management strategies for commercially fished populations that behave in this manner can be applied with the expectation of the same conversion efficiency regardless of the abundance of available food organisms.

This finding seems to be contrary to that reported under "Initial Growth of Populations." It is noteworthy, however, that the lesser efficiency at the two higher diet levels, mentioned there, occurred when the populations were stabilized at near asymptotic levels. Composition of such stabilized populations is different from that of exploited populations, and the growth reactions could well be different also.

The relation of food conversion efficiency to average size of individual fish can be examined by comparing the average weights with the food conversions for each of the nine populations during the exploitation period (weeks 59–72, data from tables 10 and 6, plus food amounts quoted above). L. M. Dickie (personal communication) has pointed out to me that if conversion efficiency be plotted as a regression on average body weight, there is a significant negative correlation (line is $E=0.317-0.667W$, where E is conversion efficiency as above, W is average body weight, and $r=-0.90$ and $P<0.01$). This determination sup-

TABLE 9.—*Weights removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
29					6.7	9.3	14.1	10.0				
30	3.6	4.9	7.0	5.2								
31												
32					7.3	6.9	8.5	7.6				
33	2.9	4.2	4.5	3.9								
34									12.8	14.2	22.2	16.4
35					5.2	5.8	5.5	5.5				
36	2.3	2.9	3.6	2.9								
37									[1] .0	9.5	14.2	7.9
38					3.4	5.2	3.6	4.1				
39	2.1	2.6	3.2	2.6								
40									[1] .0	8.3	7.3	5.2
41					3.2	4.4	3.0	3.5				
42	2.3	2.7	2.9	2.6							[2] 8.4	
43									7.4	6.8	3.5	8.7
44					5.5	6.2	7.4	6.4				
45	1.9	2.0	2.4	2.1								
46									[3] 6.5	8.4	[4] .0	5.0
47					4.1	6.1	4.5	4.9				
48	3.4	2.8	3.8	3.3								
49									1.3	3.7	6.4	3.8
50					2.3	4.0	5.6	4.0				
51	1.6	3.4	3.1	2.7								
52									6.0	7.1	5.6	6.2
53					3.3	3.2	5.6	4.0				
54	2.4	2.7	3.0	2.7								
55									[3] 10.0	5.9	6.0	7.3
56					4.9	3.6	3.1	3.9				
57	1.7	2.6	3.0	2.4					[5] .8			
58										7.1	5.0	4.3
59					3.6	4.8	2.9	3.8				
60	2.2	2.1	2.8	2.4								
61									6.2	6.1	6.6	6.3
62					4.4	4.4	4.3	4.4				
63	2.3	2.2	1.9	2.1								
64									5.8	6.5	5.5	5.9
65					4.0	4.2	3.0	3.7				
66	2.7	3.3	2.7	2.9								
67									5.0	5.7	4.5	5.1
68					4.1	3.6	2.1	3.3				
69	1.8	2.0	1.6	1.8								
70									4.8	5.2	2.7	4.2
71					2.6	2.4	2.7	2.6				
72	2.4	1.5	2.2	2.0								
Mean												
29–43	2.6	3.5	4.2		5.2	6.3	6.9		10.1	9.7	13.9	
44–58	2.2	2.7	3.1		4.0	4.6	5.2		4.9	6.4	5.8	
59–72	2.3	2.2	2.2		3.7	3.9	3.0		5.4	5.9	4.8	

[1–5] Footnotes on Table 7.

TABLE 10.—*Average biomass and yield per tank per 3 weeks for preexploitation asymptotic levels, and for levels during weeks 59 to 72. Exploitation rates are fractions removed per 3-week brood interval*

Exploitation rate	0.5 diet		1.0 diet		1.5 diet	
	Biomass	Yield	Biomass	Yield	Biomass	Yield
	G.	*G.*	*G.*	*G.*	*G.*	*G.*
0.00	[1] 14.9	0.0	[1] 26.4	0.0	[1] 41.2	0.0
0.25	[2] 9.3	[3] 2.3	[2] 13.3	[3] 3.7	[2] 17.5	[3] 5.4
0.33	[2] 7.0	[3] 2.2	[2] 10.5	[3] 3.9	[2] 16.3	[3] 5.9
0.50	[2] 3.9	[3] 2.2	[2] 6.2	[3] 3.0	[2] 8.7	[3] 4.8

[1] Taken as average of the weights for the three populations during the 3 weeks immediately preceding exploitation. Weeks were as follows: 0.5 diet, 28–30; 1.0 diet, 27–29; 1.5 diet, 32–34. Data from tables 5 and 8.

[2] Data from table 8.

[3] Data from table 9.

ports the contention (Paloheimo and Dickie, 1965) that . . . "within a life-history stanza a given food abundance leads to a higher production of replaceable fish flesh if the producing population consists of the smaller more efficient fish than if it consists of the larger fish." He further pointed out that this regression line might be the population counterpart of the "K-curve" which Paloheimo and Dickie developed for individual fish

$$(K_1=\frac{\Delta W}{R\Delta t}=e^{-a-bR},$$

where W is body weight, R is rations, and a and b are empirical constants).

The fact that the "K-curve" is an exponential relation, whereas the guppy relation is linear, may stem from the wide range of sizes of individual fish in the guppy populations (about 10–40 mm. in length). It may also result from the chief method of population control among guppies—cannibalism. This behavior causes the food of the larger fish to pass through two or more trophic levels, with a consequent lowering of conversion efficiency. Obviously, such an effect would be the more pronounced the larger the average size of individual fish in the population, as long as smaller fish are present for prey, as was true for all populations during the exploitation period.

SUMMARY

1. Nine experimental populations of the guppy, *Lebistes reticulatus*, were established in 20-l. aquariums.

2. Groups of three populations selected by lot were fed at rates 0.5, 1.0, and 1.5 times the "standard" diet.

3. Amount of food, temperature, space, and light were held constant during the course of the experiment.

4. During weeks 21 to 28 of the experiment, mean weights of populations at the 0.5, 1.0, and 1.5 diet levels were 14.5, 26.0, and 36.6 g., respectively; mean numbers of fish were 110, 145, and 149.

5. The greater mass of the populations at the higher diet levels than at the lowest reflected faster growth more than better survival.

6. Exploitation of the populations in each diet level group of three was applied at rates of 0.25, 0.33, and 0.50 per 3-week reproductive period. There were, thus, nine diet-exploitation combinations. Exploitation was started during weeks 29 to 34, when the composition of the populations was reasonably stable, and continued to the end of the experiment during weeks 70 to 72.

7. Populations responded to exploitation with an initial drop in numbers and weight, followed by near stability in weight at new lower levels (numbers were less stable, owing to entrance and mortality [through cannibalism or otherwise] of broods of new-born fish).

8. Yields in weight during the final 14 weeks of the experiment were reasonably stable and were used in the study of the interaction between food level and exploitation.

9. Curves of yield as related to biomass and exploitation rate at each diet level showed that the relation of yield to exploitation rate was independent of diet level.

10. Yields were maximum near the 0.33 exploitation rate for all diet levels, and absolute amounts were 2.4, 3.9, and 5.8 g. per 3-week period for the 0.5, 1.0, and 1.5 diets, respectively.

11. The maximum yields represented conversion of about 25 percent of the food consumed, for all three diet levels.

12. Results suggest that, to the extent that commercially fished populations behave similarly to the laboratory populations, management strategies may be applied regardless of abundance of food organisms.

ACKNOWLEDGMENTS

Most of the initial stock of guppies was donated from an aquarium maintained by Julius Rockwell, Jr. Part of the stock remained from experiments performed by Nancy Maynard. John Pricci, William Frazier, and Josephine Dickens fed and maintained the fish (all five of these people were members of the Bureau of Commercial Fisheries). L. M. Dickie and his staff of the Fisheries Research Board of Canada furnished useful suggestions which were followed in revising the manuscript.

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MODELS OF OCEANIC MIGRATIONS OF PACIFIC SALMON AND COMMENTS ON GUIDANCE MECHANISMS[1]

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ABSTRACT

The general oceanic distribution and migratory behavior of Pacific salmon are summarized, and a model of the entire migration is developed for each of three typical stocks. The pink salmon of southeastern Alaska and British Columbia circle the Gulf of Alaska counterclockwise within an area generally bounded on the west by long. 155° W. and on the south by lat. 41° N. They travel generally "downstream" in the Alaskan Gyre and the associated currents. The pink salmon of the Karaginski district on East Kamchatka also apparently make a counterclockwise circuit of the Bering Sea and North Pacific Ocean in an area bounded approximately on the west by long. 155° E., on the south by lat. 40° N., on the east by long. 150° W., and on the north by lat. 60° N. Their migratory circuit is generally "downstream": southward in the East Kamchatka Current, eastward in the Subarctic Current, and finally westward and northward in the Alaskan Stream and the Bering Sea Gyre. The sockeye salmon of Bristol Bay make two or three counterclockwise circuits in the Bering Sea and North Pacific Ocean within an area bounded approximately on the north by lat. 60° N., on the west by long. 165° E., on the south by lat. 45° N., and on the east by long. 140° W. The number of circuits depends upon the number of winters spent by the salmon at sea. In general, they travel "downstream" in the major current systems within the area defined. The time schedule, rate of travel, and average size of the fish at various stages are described for each of the three stocks.

On the basis of this summary, we believe that the salmons' migrations could not be performed if they migrated or drifted at random, or if they depended on memorized visual or olfactory cues except for final location of the home estuary and stream. The salmon predominantly travel actively with the residual ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. Also, ocean currents produce electric potentials in a range that some fish can detect; therefore, salmon might depend for navigation on electromagnetic cues from ocean currents. Furthermore, their responses to all migratory cues must be inherited, not memorized.

The return of the salmon to its home stream, to the part of the stream where its parents spawned, or even to the hatchery where it was reared as a fry has been well documented. Clearly, it is a most unusual animal migration. Not only does the salmon return to its birthplace to spawn and die, but each successive generation appears along the coast, enters the estuary, and ascends to the spawning grounds within a few days of the same schedule.

The appearance of the salmon in coastal waters and its final ascent of the stream are only the last acts in a most remarkable series of migrations that have been studied only recently in enough detail to permit a reasonably comprehensive description. The impetus for the study developed when Canada, Japan, and the United States agreed on a convention concerning North Pacific salmon which required that the high-seas migrations of major stocks of salmon near long. 175° W. and the Aleutian Islands be learned in detail. Beginning in 1955 programs were financed to study the abundance, migration, and habits of the salmon in the central North Pacific and the Bering Sea and to learn much more about their environment. These studies have expanded to include the range of the salmon on both sides of the North Pacific, so that

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[1] Contribution No. 269, College of Fisheries, University of Washington.

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now there are available reasonably complete data on the abundance and distribution of the salmon and on their North Pacific environment (Hartt, 1962; Ridgway, Klontz, and Matsumoto, 1962; Fukuhara, Murai, LaLanne, and Sribhibhadh, 1962; Callaway, 1963; Dodimead, Favorite, and Hirano, 1963; Mosher, 1963; Favorite and Hanavan, 1963; Amos, Anas, and Pearson, 1963; Margolis, 1963; Kasahara, 1963; Manzer, Ishida, Peterson, and Hanavan, 1965; Godfrey, 1965; Mason, 1965; Tanaka, 1965; Kondo, Hirano, Nakayama, and Miyake, 1965; Hartt, 1966).

The abundance and distribution of salmon at sea are dynamic and variable. The salmon occupy almost all of the North Pacific Ocean north of about lat. 41° N. in the winter or lat. 48° N. in the summer and all of the Bering Sea south of the ice pack. They are found mostly in the upper 10 m.—far from any contact with the bottom. The maturing individuals, which are due in their spawning streams sometime between June and December, begin to move rapidly 1 to 2 months before their arrival dates and commonly maintain average speeds of 30 miles (55 km.) per day [2] for many hundreds of miles. Major numbers of several groups of salmon may, thus, pass through a particular ocean area within 3 weeks. The immature salmon, which remain in the ocean at least another year, commonly undertake extensive feeding migrations generally in a counterclockwise circular pattern that is repeated annually. The salmon of the different species are usually mixed. The mature and immature salmon of one species are sometimes mixed and sometimes segregated. The different stocks of a single species commonly vary as much in their distribution as do the different species, although in the early spring sockeye salmon (*Oncorhynchus nerka*) tend to predominate at the northern boundary of salmon waters and pink salmon (*O. gorbuscha*) at the southern.

The information on ocean migrations is as yet only fragmentary, partly because of the difficulties and expense of working in the autumn and winter and partly because of the lack of suitable gear and techniques for the study of the distribution and migrations of the young salmon after they have left the estuary. We do have enough information, however, on some important stocks to describe their migrations in considerable detail and to make some inferences to fill the gaps in our information. We shall undertake, therefore, to construct models of the ocean migrations of three typical stocks originating in diverse geographical areas: southeastern Alaska and central British Columbia pink salmon: East Kamchatka pink salmon; and Bristol Bay sockeye salmon. Substantial information is available on these stocks, and all three are large enough to have been identifiable in the ocean with reasonable certainty. Fragmentary data on other stocks and species agree with these in principle. The models will illustrate the features of the migration, the navigational problems of which we are now aware, and the kinds of position- and direction-finding information that we presume are available to the salmon.

Our discussion rejects or extends and complements the summaries and hypotheses about high-seas migrations that some authors have set forth recently. We reject the general applicability of the hypothesis about random movement of salmon suggested by Saila and Shappy (1963). We extend the hypotheses about electric navigation presented by Waterman (1959). We extend with new information the thorough review of the oceanic migrations of Pacific salmon by Neave (1964). We question and limit the applicability of sun-compass and odor-perception mechanisms hypothesized by Hasler (1966); Hasler, Horrall, Wisby, and Braemer (1958); and Hasler and Schwassmann (1960).

Perhaps our information concerning salmon migration will help to explain the mechanisms used by other aquatic species that undertake long-range oceanic migrations and about which much less is known. In the Pacific these fishes now include the albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), bluefin tuna (*Thunnus saliens*), black cod (*Anoplopoma fimbria*), and dogfish (*Squalus acanthias*); numerous species of marine mammals and turtles also are known to migrate extensively at sea.

The migrations of the salmon begin when the fry emerges from the gravel. These first few inches of migration through the gravel may well be the most hazardous of its entire life. It then moves downstream (or occasionally upstream) to sheltered waters. Coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) usually find shelter and food in rivers and streams; sockeye salmon in lakes; chum salmon (*O. keta*) and pink salmon in salt-water estuaries and bays. The physiological change from fresh water to salt water is highly significant, but the ecological change is not. The young salmon needs a place with food and protection from its enemies, and this it finds along the shores of lake, river, or estuary. After it reaches a length of about 5 to 8 cm. it may move to bigger waters where the feeding is better, and at a size of 10 to 15 cm. it usually seeks the open sea. This is where our story of the ocean migrations begins.

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[2] The miles used throughout this paper are nautical miles.

OCEAN MIGRATIONS OF PINK SALMON OF SOUTHEASTERN ALASKA AND BRITISH COLUMBIA

Of the Pacific salmons, pink salmon probably have the least complicated oceanic migrations because of their short and uniform 2-year life history. The pink salmon stocks about which we have the most comprehensive knowledge of migrations are those of southeastern Alaska and British Columbia originating between Cape Flattery, Wash. (lat. 48° N.), and Cape Spencer, Alaska (lat. 58° N.)—figure 1. Washington State pink salmon form part of these stocks in odd-numbered years. Spawning takes place from mid-July to mid-October, but tends to be earlier in the more northerly areas. Fry emerge from the gravel from February through June; the peak period is in April and May (Sheridan, 1962; Neave, 1966). The fry immediately migrate downstream to salt water and then feed in schools along the shores of estuaries and bays for 2 or 3 months. As they attain a size of 5 to 6 cm., they venture farther offshore.[3] They migrate to the ocean proper in July, August, and September, at a length of 12 to 15 cm. (Gilhousen, 1962; Neave, 1966; Hartt, Dell, and Mathews, 1966).

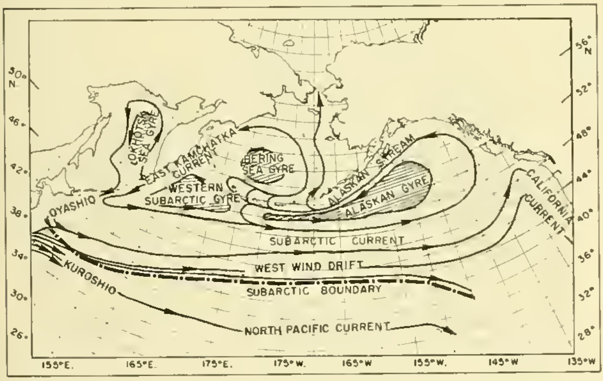

FIGURE 1.—Base map of North Pacific area and surface circulation (adapted from Dodimead et al., 1963, fig. 109).

The ocean migratory period of these stocks, typical of that of pink salmon, extends approximately from July of the year after spawning until summer or early autumn of the next year. On the basis of recent research, we can now describe or hypothesize within moderate limits of dependability the migrations of the southeastern Alaska and British Columbia pink salmon throughout essentially all stages of their 12 to 14 months at sea.

SUMMER EMBARKATION

Juvenile pink salmon enter the ocean proper at numerous points along the southeastern Alaska-British Columbia coast during July, August, and September; their abundance apparently peaks in August (Martin, see footnote 3; Hartt et al., 1966). They do not scatter randomly seaward, but turn northward and migrate along the coast in a narrow band extending about 20 miles (37 km.) offshore (Hartt et al., 1966). They continue in this manner around the northern periphery of the Gulf of Alaska and southwestward past Kodiak Island. The band widens, in the northern part of the Gulf, presumably because there the Continental Shelf is wider. Stocks other than those from southeastern Alaska and British Columbia undoubtedly join the procession off Prince William Sound, Cook Inlet, and Kodiak Island (Hartt, Smith, and Dell, 1967).

The width of the band and the northerly direction of migration were determined by fishing a large, fine-meshed purse seine at various distances from shore and by facing the net in opposed directions. The seine was set in a semicircle, held open for 30 minutes, and then closed to collect fish migrating toward the opening of the seine. Catches were large when the seine was held open to the southeast and small when open northwest (Hartt et al., 1966). For example, in 1964 off southeastern Alaska, the average catch was 350 fingerlings when the seine was open southeast and zero when it was open northwest.[4] A time-space extrapolation of the average catch (in 30 minutes in a $\frac{1}{4}$-mile-wide [0.46-km.] band) indicated that at least 750,000 juveniles migrated daily past any given line of latitude off southeastern Alaska in 1964. Thus, for the 30 to 60 days of strong migration, it is evident that major stocks of fish were involved.

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[3] Martin, John W. 1964. Studies of estuarine and inshore marine ecology of juvenile pink salmon in southeastern Alaska. *In* W. J. McNeil (editor), Report of the 1964 northeast Pacific pink salmon workshop and contributed papers. U.S. Fish Wildl. Serv., Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska, Manuscript Rep. 64–5: 80–83.

The fork length of the pink salmon at this stage varies from 10 to 25 cm. The average size was significantly larger in the northern samples, presumably because of the presence of fish which had already migrated a considerable distance from southern production areas (fig. 2). The northern samples also included small fish that presumably had just entered the sea from nearby channels and bays. Mixed with the juvenile pink salmon were juvenile sockeye, chum, coho, and chinook salmons and steelhead trout (*Salmo gairdneri*), which suggests that the migratory cue at this stage is similar for all species.

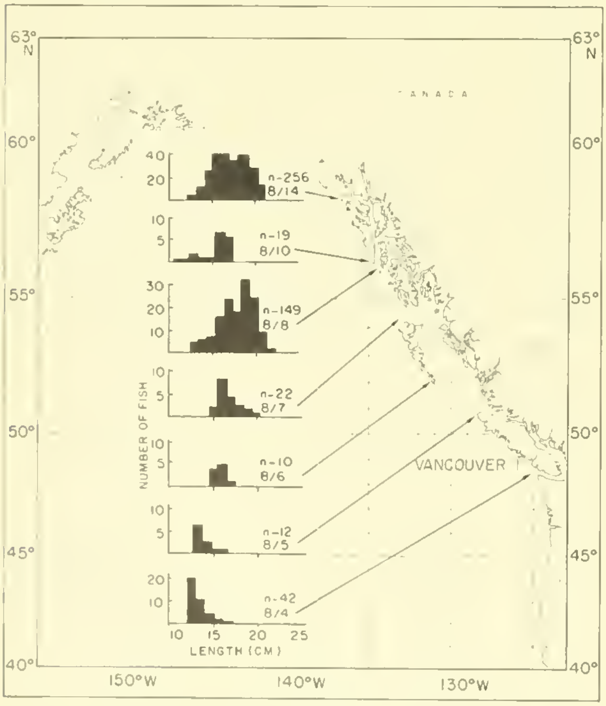

FIGURE 2.—Fork lengths of juvenile pink salmon sampled August 4–14, 1964, in eastern Gulf of Alaska.

The northward migration of juvenile salmon is indicated by the purse-seine catches and tag returns. Six pink salmon were recovered a year after tagging, all in southeastern Alaska (fig. 3). All were recovered south of the point of release. If it is assumed that they entered the ocean near the point where they were recaptured as maturing fish, they must have migrated northwestward before they were tagged. The specimen tagged near lat. 59° N. by long. 138° W. had traveled about 350 miles (648 km.) by September 22, 1961, when it was tagged. Figure 3 also illustrates the locations of release and recovery for 1 sockeye salmon, 1 steelhead trout, and 58 coho salmon that were tagged as juveniles, along with the pink salmon.

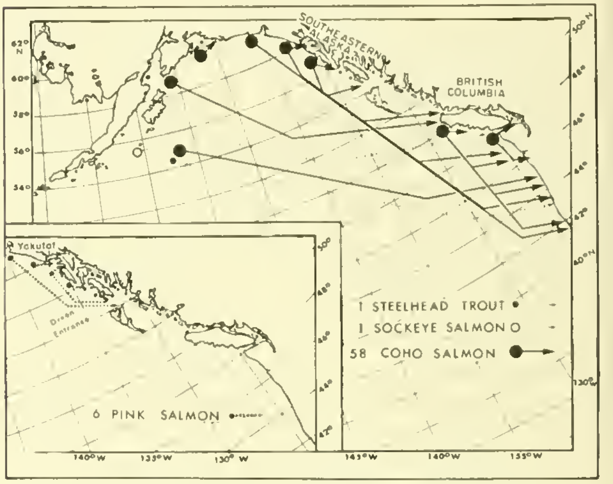

FIGURE 3.—Release and recovery diagram of salmon and steelhead trout tagged as juveniles and recovered 1 or 2 years later (all coho and pink salmon were recovered 1 year after tagging).

These fish were also recovered south of the points of release; some traveled northwestward over 1,000 miles (1,852 km.) before they were tagged.

The rate of travel of juvenile pink salmon during their first few months at sea is difficult to estimate on the basis of the few tag returns received to date, because the distances involved are relatively short and the date of ocean embarkation can only be approximated. If we assumed that the specimen tagged near Yakutat (fig. 3) on September 22 had left Dixon Entrance on August 1, and then had followed the coastline (350 miles or 648 km.), its rate of travel would be 6.6 miles (12.2 km.) per day. By the same method, if we assumed that the sockeye and coho salmons and the steelhead tagged south of Kodiak Island had embarked as juveniles on May 1, then they each covered about 1,400 miles (2,593 km.), in about 4 months preceding tagging, at an average rate of 11.6 miles (21.5 km.) per day. The May 1 embarkation date is probably correct for the steelhead trout; it was fin-clipped and released in the Alsea River, Oregon, sometime in April 1958. The estimated rates of travel of the latter three juveniles are probably more accurate than the estimated rate of travel of the single pink salmon, so that 10 miles (18.5 km.) per day might be a good working estimate of rate of travel during the initial stage of their ocean migrations.

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[4] For a discussion of the validity of purse seine gear for determining directional migrations of salmon in areas of strong ocean currents, see Hartt (1966: 8–10).

AUTUMN AND WINTER MIGRATIONS

We have much less data on the autumn and winter migrations, but the general pattern can be deduced from the substantial data on the location of juveniles in late summer and of maturing fish in early spring. By late September, most pink salmon have entered the sea, but substantial numbers still are along the coast from southeastern Alaska to Kodiak Island; juvenile migration must continue, therefore, into October and November. Neave (1964) reported 163 juvenile pink salmon in a trawl catch in Dixon Entrance (lat. 54° N.) on November 5, 1963. After the end of September, the next period for which there are data is January–February, when longlines and gill nets have been fished in recent years, although somewhat sparsely, throughout much of the Gulf of Alaska.[5] Results in 1964 indicated few, if any, pink salmon in the northern Gulf but a wide dispersion in the southern Gulf between lat. 45° and 51° N. and from about long. 133° to 156° W. (fig. 4). At this stage they average 30 cm. long (French, 1966: International North Pacific Fisheries Commission, Annual Report, 1964: 30).

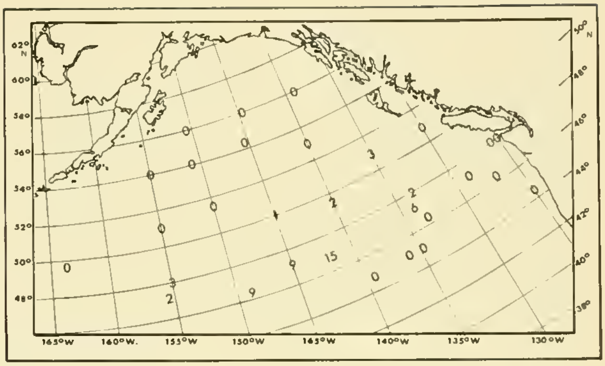

FIGURE 4.—Catch of pink salmon per longline set during winter of 1964. Canadian and United States operations January 7 to February 9 (30 sets, each using 5 to 35 skates—one skate=49 hooks).

Thus, between midautumn and midwinter, the young pink salmon must leave the coastal belt along the northern Gulf and migrate well to the south, where they are scattered widely in the open sea. The points at which they leave the coastal belt are unknown. They probably do not follow the Alaskan Stream very far to the west, however, because immature pink salmon have never been taken in the extensive seining in the summer and autumn south of the eastern Aleutian Islands. Furthermore, extensive tagging of mature pink salmon in spring and summer south of the Aleutians has yielded returns only from East Kamchatka and western Alaska; none were returned from southeastern Alaska or British Columbia nor from any other Gulf coastal areas. Thus, the stocks in question probably leave the coastal belt east of long. 160° W. Such a southward migration would place them in the eastward-flowing Subarctic Current, on a counterclockwise route back toward their embarkation points (fig. 1). The distance from the northern Gulf to the center of their winter distribution is at least 1,000 miles (1,852 km.), which, if covered in 90 days, would indicate a minimum rate of travel of 10 miles (18.5 km.) per day.

SPRING-SUMMER HOMING MIGRATIONS

The ocean migrations of the maturing pink salmon during their last spring and summer at sea are well documented by a number of years of longline and purse seine sampling throughout the Gulf from late March through mid-August (Neave, 1964; International North Pacific Fisheries Commission Annual Reports, 1961–65). In April pink salmon of the southeastern Alaska-British Columbia stocks are located mainly in the southeastern part of the Gulf east of long. 150° W. and between lat. 43° and 50° N. and are mixed with stocks from Prince William Sound, Kodiak Island, Cook Inlet, and the Alaska Peninsula. The British Columbia stocks are farthest to the east—mainly east of long. 135° E. (Fisheries Research Board of Canada, 1962–66).

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[5] For convenience, *Gulf of Alaska* as used herein refers to all salmon waters east of long. 165° W., thus extending to about lat. 40° N., in conformance with the general oceanic regions described by Manzer et al. (1965).

During May and June, pink salmon shift progressively northward in the eastern half of the Gulf and by July are abundant in the northernmost areas (fig. 5). The early-run stocks then migrate toward their respective coastal destinations. Later-run fish frequently return to the southeast in August and September after having migrated northward past their area of origin (Neave, 1964). For these fish the late-season homing migration follows in reverse the coastwise route taken by the juveniles in the Alaskan Gyre and is "upstream" instead of "downstream." Returns of tagged fish to southeastern Alaska and British Columbia in 1962 (fig. 6) illustrate the spring-summer distribution and migrations of these stocks.

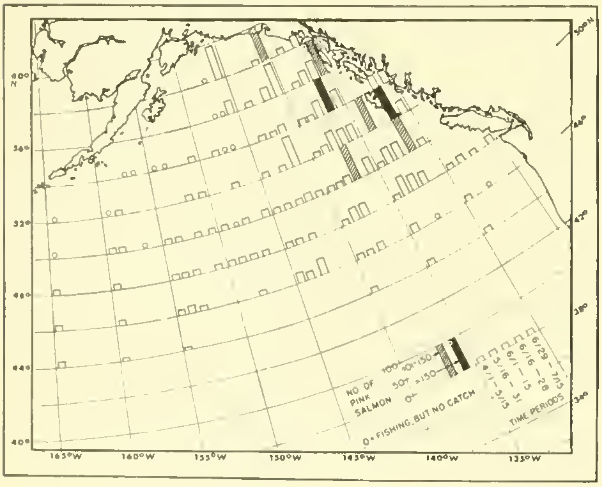

FIGURE 5.—Average catch of pink salmon per 20 skates of longline gear (49 hooks per skate) by area and by time period in 1966 (U.S. and Canadian data unpublished).

The rate of movement of the center of abundance from mid-April to mid-June appears to be about 7 miles (13 km.) per day (if movement is estimated from lat. 48° to 55° N. during the 60-day period). Rates of travel of individual tagged fish based on straight-line distances to recovery points vary from 5 to over 40 miles (9.3–74.1 km.) per day. Mean fork lengths at this stage vary from 45 to 55 cm., or even larger for late-season spawners.

The final migrations through channels and bays to the natal streams need not be reviewed in this paper except to note that coastal tagging indicates considerable "searching" or "to and fro" migrations as the numerous stocks approach their home estuaries (Noerenberg, 1959; Verhoeven, 1952).

SUMMARY

The oceanic migration of southeastern Alaska-British Columbia pink salmon is shown diagrammatically in figure 7 according to four time periods. The western limits and the southern limits are only approximate. After spending 3 to 5 months in estuaries and inner bays and channels, juvenile pink salmon enter the ocean proper in July to September at a length of 10 to 15 cm. They travel rapidly northward and westward along the coast, following the Alaskan Gyre. By late September and early October they average 20 to 22 cm. long. Their average rate of travel is about 10 to 12 miles (18.5–22.2 km.) per day. Between October and midwinter they migrate southward and in January to February are spread widely between lat. 41° and 51° N. and from long. 130° to 160° W. and have continued to migrate at least 10 miles (18.5 km.) per day. At this stage the mean length is 30 cm. In their final spring and summer, they migrate northward in the eastern Gulf from April through July, then coastward to their respective destinations; the late-spawning stocks turn back southeastward to return to their areas of origin. Mean sizes at maturity vary from 45 to 55 cm. Rates of travel in final coastward migrations are at least 10 miles (18.5 km.) per day; some individuals migrate over 45 miles (83.3 km.) per day.

OCEAN MIGRATIONS OF PINK SALMON OF EAST KAMCHATKA

Although data are fewer on the ocean migrations of East Kamchatkan pink salmon than for the southeastern Alaska-British Columbia stocks, the probable sequence of migration can be inferred and certain similarities and contrasts indicated.

The East Kamchatkan stocks (mainly the Karaginski district, fig. 8) are substantial, over 40 million adults in some odd-numbered years.[6] The spawning migration in the Karaginski region is

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[6] From: "Pacific salmon catch statistics of the Union of Soviet Socialist Republics 1940–1958" (plus similar tables for individual years 1959–64), as given to the International North Pacific Fisheries Commission by the All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, unpublished.

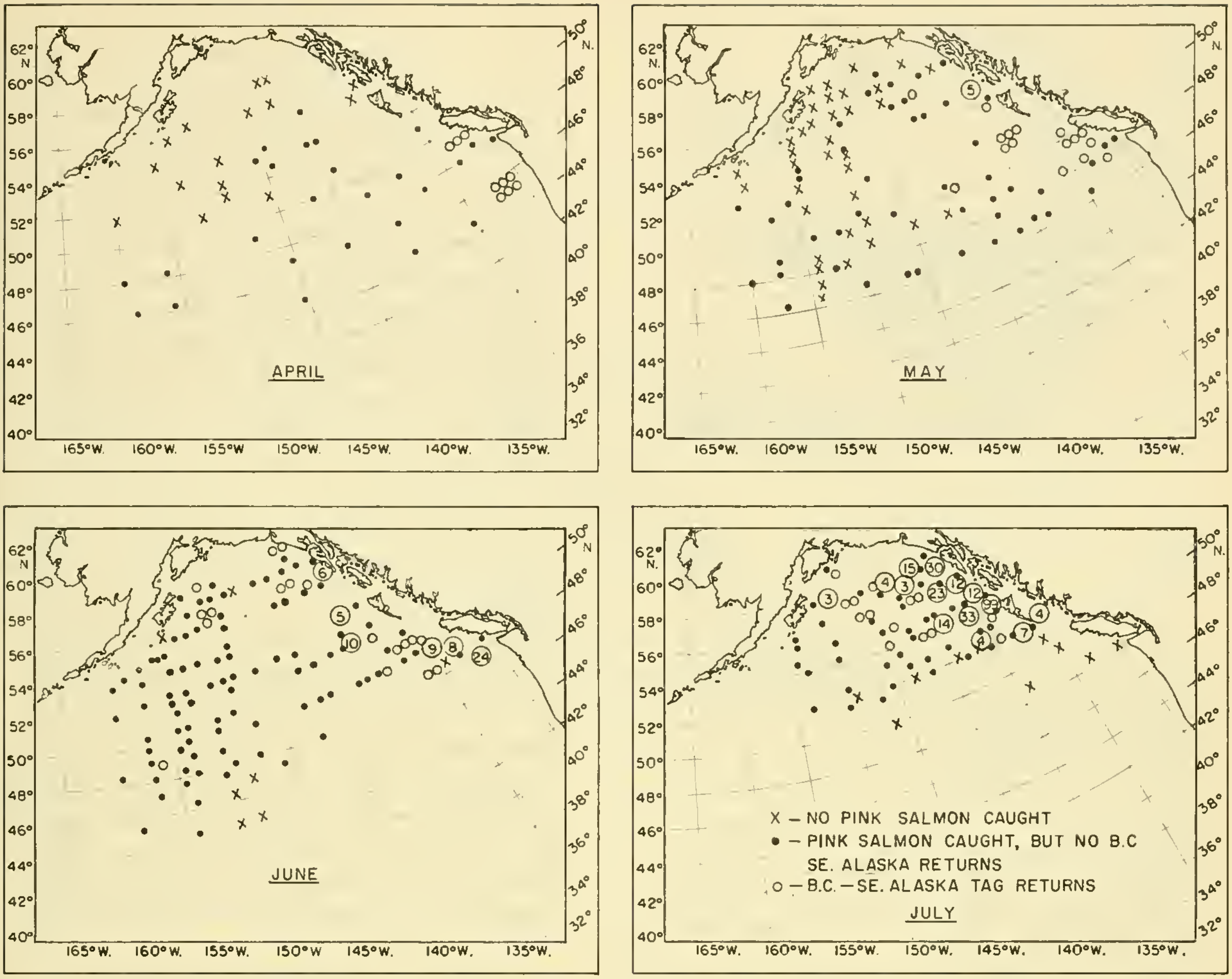
APRIL
MAY
JUNE
JULY
X – NO PINK SALMON CAUGHT
• – PINK SALMON CAUGHT, BUT NO B.C SE. ALASKA RETURNS
○ – B.C. – SE. ALASKA TAG RETURNS
165°W.
160°W.
155°W
150°W.
145°W.
140°W.
135°W.
62° N.
40°
50° N.
32°

FIGURE 6.—Spring-summer distribution of southeastern Alaska-British Columbia pink salmon in the Gulf of Alaska in 1962 as shown by longline and purse seine catches and by tag returns (source: Canadian and U.S. data, International North Pacific Fisheries Commission Annual Report, 1962).

relatively brief and occurs principally in July (Kaganovskiĭ, 1949). The fry probably migrate to sea in June, but data are lacking.

If the East Kamchatkan pink salmon respond to ocean currents as do the southeastern Alaska-British Columbia stocks, then they may be expected to follow the East Kamchatka Current southwestward along the coast and then to migrate eastward with the Subarctic Current and the Westwind Drift (fig. 1). Their presence in the western Gulf of Alaska (near lat. 50° N. and long. 155° to 160° W.) in May and June has been demonstrated by tag returns (Fisheries Research Board of Canada, 1963; Hartt and Dell, 1964). Their presence south of the entire Aleutian chain from late May through early July and in the Bering Sea in June and July has also been well demonstrated by Japanese and United States tagging (Hartt, 1962; Kondo et al., 1965). Purse seining by the United States has further shown that they move very rapidly in a westward direction south of the Aleutian Islands, northward through the major passes, and northwestward in the Bering Sea. Passage south of the central Aleutians peaks sharply about June 5 to 30.

The rate of travel to the Karaginski district from the central Aleutians (about 800 miles or 1,482 km.) averages about 25 to 30 miles (46.3–55.6 km.) per day for the last 30 to 45 days at sea (Hartt, 1966). Thus, the migration is more

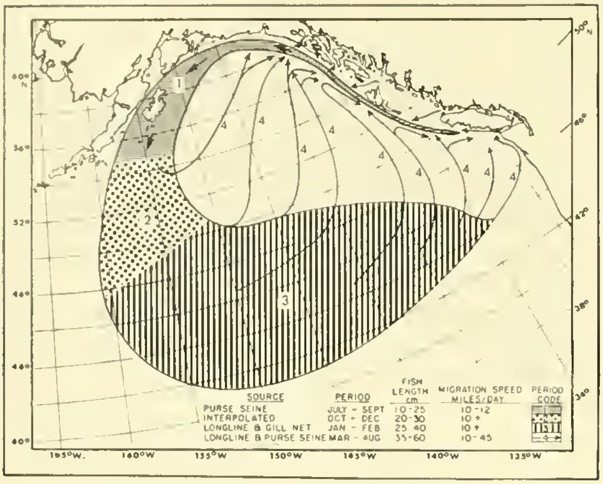

FIGURE 7.—Diagram of ocean migrations of pink salmon stocks originating in southeastern Alaska and British Columbia.

directed and rapid than that of the southeastern Alaska-British Columbia pink salmon, perhaps because the East Kamchatka stocks have a more limited time of arrival.

Recoveries of tagged pink salmon at sea suggest that the fish migrate rather directly toward their coastal destination from the point of release (fig. 8). Ishida (1960) suggested that the fish apparently follow parallel courses toward the Karaginski district from whatever point they enter the Bering Sea. Such an ability to navigate toward "home" is in agreement with Neave's thesis (1964) that to perform the observed migrations salmon at sea must maintain "bico-ordinate orientation" (i.e., oriented with respect to "home" in two components such as east-west and north-south).

The postulated migration of East Kamchatka pink salmon is diagrammed in figure 9. The first two steps—migration downstream in the East Kamchatka Current and in the Subarctic Current and Westwind Drift—are assumed (figs. 1 and 9). Direction appears to change abruptly as they depart the eastward-flowing Subarctic Current and join the westward-flowing Alaskan Stream. The influence of the Bering Sea Gyre on the migration route is unknown, but the tagging data illustrated in figure 8 indicate that migration continues rather directly through the Gyre.

A significant feature of the migration of the Karaginski pink salmon is that throughout much of their route during their last 60 to 90 days at sea they are intermingled little with other pink salmon stocks although they are extensively intermingled with sockeye and chum salmon. In the western part of their distribution they are mixed with West Kamchatka and other Sea of Okhotsk stocks, and in the eastern extreme they mix with Gulf of Alaska stocks (Hartt, 1966). In the central part of their oceanic range they are mixed only with the relatively minor Aleutian and western Alaska stocks. Tagging data indicate that their distribution is probably just as extensive in even-numbered years of low abundance as in odd-numbered years of high abundance. In addition, the abundant West Kamchatka or Gulf of Alaska stocks do not move into the central Aleutian area in years when the East Kamchatka stocks are scarce (Hartt, 1966; Kondo et al., 1965). These observations indicate that oceanic-migration patterns are independent of abundance within or between individual stocks.

OCEAN MIGRATIONS OF SOCKEYE SALMON OF BRISTOL BAY

Bristol Bay stocks are defined herein as those originating in the eastern Bering Sea between the northern side of Unimak Island and the Kuskokwim River (fig. 10): fish originating within this area migrate similarly at sea. Nearly all originate in five main river systems—Nushagak, Kvichak, Naknek, Egegik, and Ugashik—which enter at the head of Bristol Bay near lat. 58° N., long. 157° W. (fig. 10). These stocks make up the largest sockeye salmon run in the world, between 6 and 60 million mature fish per year. The annual average for 1956–65 was 23.9 million (Ossiander, 1965; Pacific Fisherman, 1966).

The life history of Bristol Bay sockeye salmon, although variable, may be described in general as follows. Spawning takes place in August and September in the vast Bristol Bay lake systems. Fry emerge mainly in June. The young fish generally spend 1 or 2 winters in fresh water and migrate to sea as 2- or 3-year-old smolts. Downstream migration is mainly in June, simultaneously with or immediately after breakup of the lake ice. Most then spend 2 or 3 years at sea so that their total age at maturity is usually 4, 5, or 6 years with various combinations of fresh-water and salt-water age. The returning run migrates through the estuaries from about June 20 through July 25, but

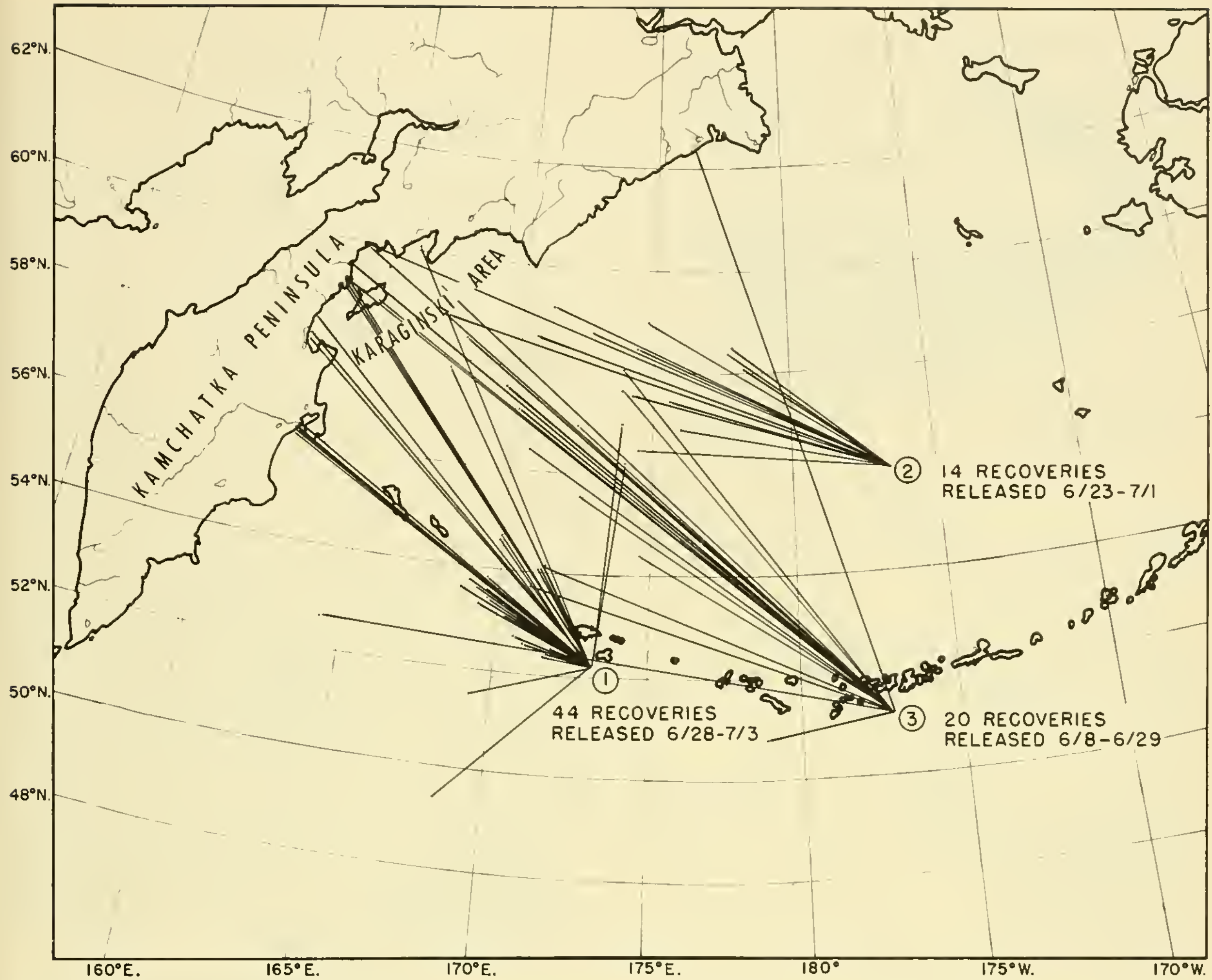
62°N.
60°N.
58°N.
56°N.
54°N.
52°N.
50°N.
48°N.
KAMCHATKA PENINSULA
KARAGINSKI AREA
② 14 RECOVERIES
RELEASED 6/23-7/1
① 44 RECOVERIES
RELEASED 6/28-7/3
③ 20 RECOVERIES
RELEASED 6/8-6/29
160°E.
165°E.
170°E.
175°E.
180°
175°W.
170°W.

FIGURE 8.—High-seas and coastal recoveries of pink salmon tagged at three points in the North Pacific Ocean and Bering Sea in 1959.

over 80 percent of the run arrives within 9 to 22 days, and this arrival period occurs regularly between June 23 and July 18 (Royce, 1965). The peaks of the run vary only from July 2 to July 9.

The ocean migrations of the Bristol Bay sockeye salmon have been studied intensively more than 10 years (International North Pacific Fisheries Commission, 1957–66). Excellent data are available for the spring and summer periods, and some winter data are available, so that the entire migratory pattern can be inferred.

FIRST YEAR AT SEA

The smolts from the five main river systems enter the coastal waters of Bristol Bay in an intensive mass migration that peaks sharply during June. Their length at this stage typically ranges from 7 to 12 cm., varying according to river system and fresh-water age. During July, they travel at least as far westward as long. 164° W. (250 miles [463 km.] from the Naknek-Kvichak estuary) and are apparently most abundant near the Alaskan Peninsula. Observations at this stage are based on limited purse seining in 1962 and 1966 (unpublished). Purse seine catches ranged up to 1,300 fish per set. At this stage they feed heavily on euphausids and larval fish and grow rapidly; the average size of those in the westernmost samples ranged from 13 to 15 cm. in July.

After this early marine stage, data on their migrations are few until they appear a year later

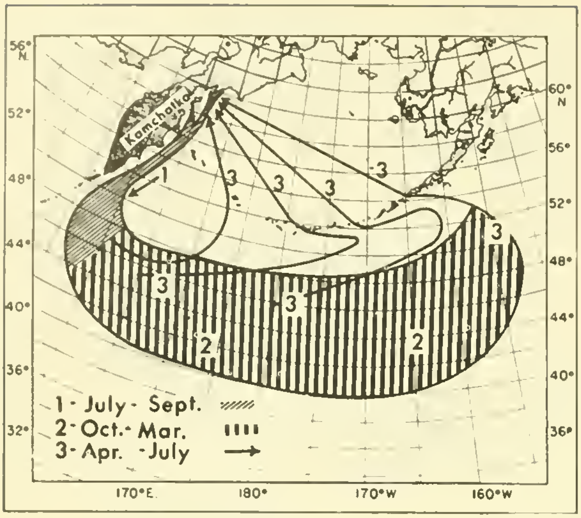

FIGURE 9.—Diagram of probable ocean migrations of pink salmon stocks originating in East Kamchatka.

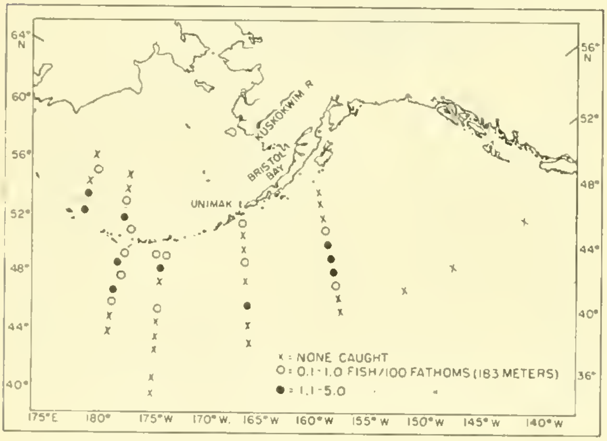

FIGURE 10.—Catches of .1-age sockeye salmon during winter gill netting in 1962 and 1963 (source: French and Mason, 1964).

as .1-age[7] immature fish of 35-cm. average length migrating westward in large numbers along the south side of the Aleutian Islands. Two items of indirect evidence, however, help fill in the first year's migration. First, the Bristol Bay sockeye salmon apparently do not migrate south of the Aleutians during their first summer; .0-age juveniles were extremely rare in the intensive purse seine sampling along the south side of the Aleutians during the summers of 1956–65 (International North Pacific Fisheries Commission, 1957–66). Second, winter sampling with gill nets (French and Mason, 1964) has shown the presence of .1-age sockeye salmon north of the western Aleutians and south of the central Aleutians during January and February (fig. 10). At this stage they average about 25 to 30 cm. long. It has not been proved that these are Bristol Bay fish, but it seems safe so to assume, because of their abundance and because tagging and other studies have shown that Bristol Bay stocks predominate in these areas in spring and summer. Thus, we may postulate that the fingerlings remain in the Bering Sea at least until autumn, and their winter distribution suggests that they reach the western Bering Sea and proceed southward into the North Pacific. The next move must be eastward in the Subarctic Current to place them in position by late spring to make the characteristic summer migration westward with the Alaskan Stream along the south side of the Aleutian Islands—a migration which has been extensively studied and described (Hartt, 1966). The postulated first year's migration is diagrammed in figure 11A as part of the schematic of their entire ocean travels. The first year's migration could be accomplished at an average rate of 10 miles (18.5 km.) per day, which is the rate indicated for the juveniles tagged near Kodiak Island in the Gulf of Alaska discussed earlier.

SECOND YEAR AT SEA

During their second summer at sea, Bristol Bay sockeye salmon are immature .1-age fish averaging 35 cm. long. They migrate westward south of the Aleutian Islands in a more or less continuous band, from late June through mid-September. The band extends offshore about 100 miles (185 km.), but the greatest abundance is usually within 30 miles (55.6 km.) (French, 1964; Hartt, 1966). The fish apparently approach from areas to the south and east and continue far westward and northwestward, as shown by tag returns from the high-seas fleet in the year of release (fig. 12). The dominance of Bristol Bay stocks is demonstrated by coastal tag returns 1 year later (fig. 12) and by the relation between age composition and abundance at sea and age composition and abundance in the Bristol Bay run 1 year later (Ossiander, 1965). Some idea of the magnitude of the

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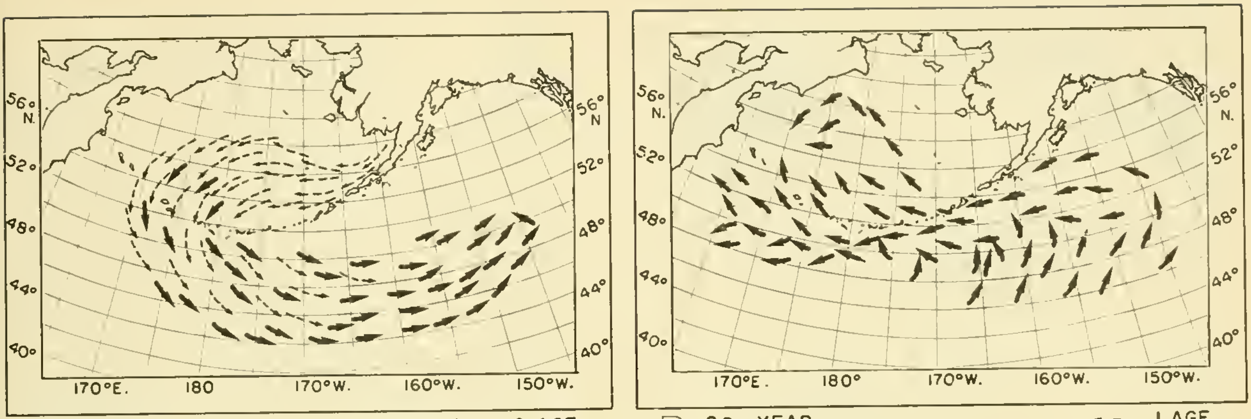
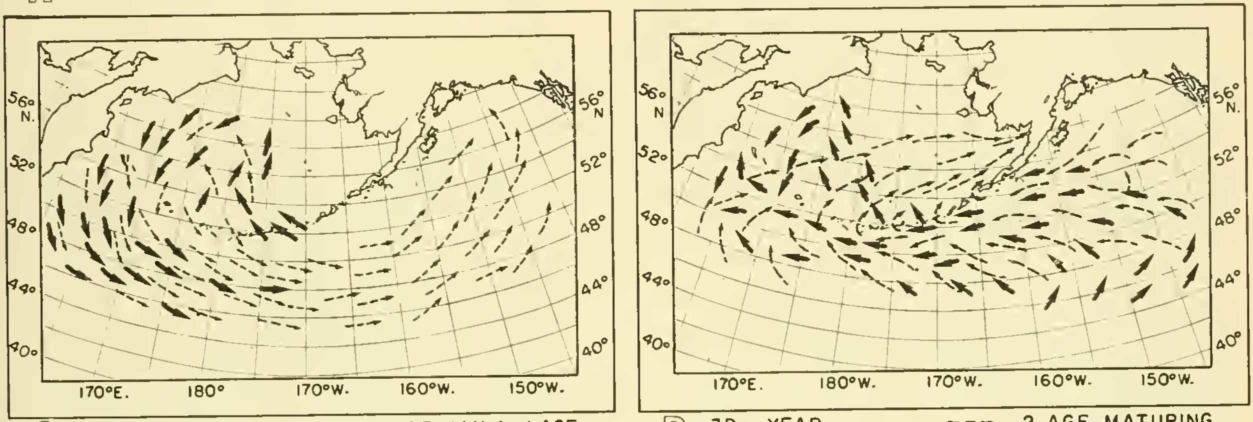
[7] Ocean age designation throughout this paper is that proposed by Koo (1962) in which the number of ocean winter annuli on the scale is preceded by a decimal point (e.g., .1-age—one winter at sea).


56° N.
52°
48°
44°
40°
170°E.
180
170°W.
160°W.
150°W.

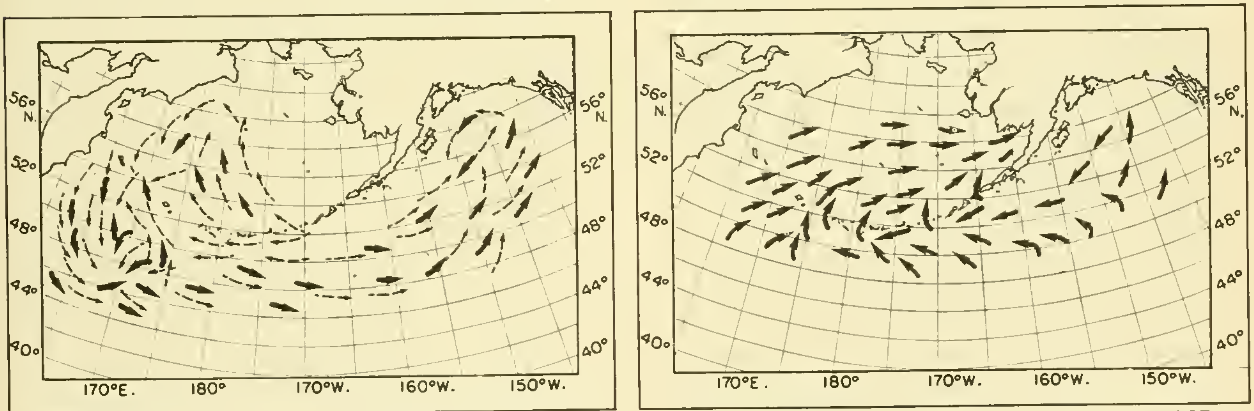
A – 1ST. YEAR JUNE 1 TO MAY 31 ---- PRIOR JAN. 1 .0 AGE ⟵ AFTER JAN. 1 .1 AGE

B – 2D. YEAR JUNE 1 TO AUG 31 ⟵ .1 AGE


56° N.
52°
48°
44°
40°
170°E.
180°
180°W.
170°W.
160°W.
150°W.

C – 2D. YEAR SEPT. 1 TO MAY 31 ⟵ PRIOR JAN 1 .1 AGE ---- AFTER JAN. 1 .2AGE (60%-80% MATURING)

D – 3D. YEAR JUNE 1 TO AUG 31 ---- .2 AGE MATURING ⟵ .2 AGE IMMATURE


56° N.
52°
48°
44°
40°
170°E.
180°
170°W.
160°W.
150°W.

E – 3D. YEAR SEPT. 1 TO MAY 31 ---- PRIOR JAN. 1 .2 AGE ⟵ AFTER JAN. 1 .3 AGE (MATURING)

F – 4TH. YEAR JUNE 1 TO AUG 31 ⟵ .3 AGE (MATURING)

FIGURE 11.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on seine catch and tagging data through 1966; arrows indicate direction and approximate distribution.

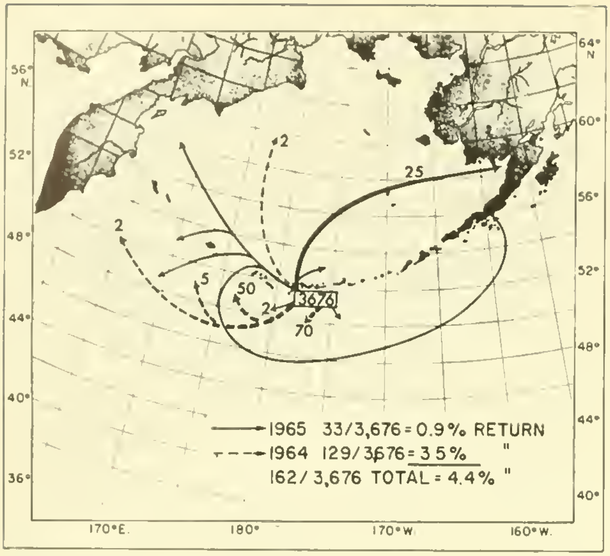


FIGURE 12.—Recovery distribution of sockeye salmon tagged as .1-age immature fish at Adak in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

numbers can be gained from a conservative time-space extrapolation of the average catch per 30-minute seine set; in 1964 a minimum of 0.5 million .1-age sockeye salmon per day passed westward south of Adak Island from late June through late August, or about 30 million of this age group alone. The rate of travel averaged 17 miles (31.5 km.) per day for those recovered by the Japanese fleet in 1964. Stomach examinations indicated that the fish feed actively on various crustaceans and larval fish (Dell, 1963). The probable summer migration of the .1-age immature fish is summarized in figure 11B.

The fact that the .1-age fish migrate past a given point for a long period indicates that they must be spread over a large area at sea. Such an extended distribution is probably characteristic of salmon in general even in their first summer, as evidenced by the long band of .0-age salmon of all species along the coast of the Gulf of Alaska described earlier. It is important to emphasize here that the .1-age immature sockeye salmon at this stage are thoroughly mixed with the .2-age immature fish that left Bristol Bay a year earlier; apparently they overtake the previous year's smolts and then follow a similar migratory path.

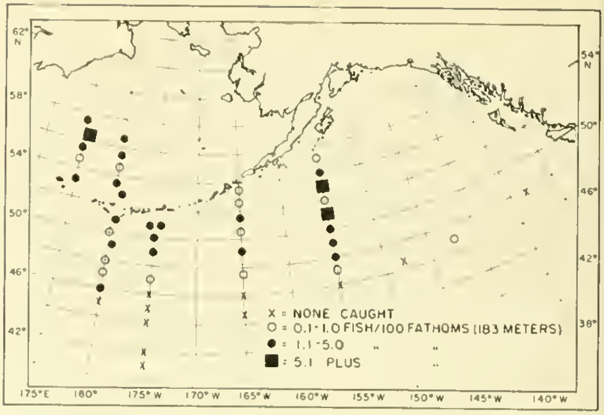


FIGURE 13.—Catches of .2-age and older sockeye salmon during winter gill netting in 1962 and 1963 (source: French and Mason, 1964).

The winter data (figs. 10 and 13) indicate that the intermingling of the age groups takes place as early as January. In general, however, the .1-age group in figure 10 was farther south than the older fish shown in figure 13. Thus, it would appear that the migration of this age group is independent of the older fish at this early stage.

The migrations during the autumn and winter of the second year at sea can be inferred from the limited winter sampling and from the distribution and migrations observed in the following spring and summer (fig. 11C). During this period the .1-age fish add another winter mark on their scales and become .2-age fish. Some will mature in this year and migrate homeward to spawn, but others will remain at sea to mature a year later at .3-age. As illustrated in figure 13, .2-age sockeye salmon are distributed widely during the winter (January–March) in the central and western Bering Sea and in the North Pacific at most sampling stations north of lat. 45° N. As at other times of the year, Bristol Bay fish may be expected to be present in most of the samples. The data then suffer a gap until the following May, when samples taken by purse seines indicate few, if any, sockeye salmon in the Alaskan Stream south of the Aleutians. In late May and early June, however, the maturing .2-age sockeye salmon begin to appear in the catches along the entire south side of the Aleutians, and they are again migrating westward in the Alaskan Stream. The evidence, thus, indicates a southward shift during late winter and early spring and a return migration toward the east in the Subarctic Current (fig. 1). The fish apparently repeat the winter-spring-summer round of migrations of their first year at sea (fig. 11A). Further support for this hypothesis is provided by the recovery in the Shumagin Islands area in the eastern Aleutians of .2-age sockeye salmon that had been tagged as .1-age immature fish a year earlier near Adak Island (fig. 12). The 1964 data are typical of other years' results. At Adak they had been part of the westward flow of immature fish, and at Shumagin Islands they were among maturing fish that characteristically migrate westward, many of them en route to Bristol Bay (Thorsteinson and Merrell, 1964).

THIRD YEAR AT SEA

The migrations during the third year at sea must be considered separately for one group that matures and returns to spawn at the end of its second year at sea (early in its third summer at sea), and another group that remains another full year at sea. From the numbers of .2- and .3-age fish returning in successive years, about 60 to 80 percent of the .2-age group mature and spawn. The fish of the maturing group average about 51 to 53 cm. in fork length and are thoroughly mixed with the older .3-age mature salmon. They approach the eastern Aleutian Islands area from the south and southeast in late May, migrate westward with the Alaskan Stream, northward through the Aleutian passes, and then northeastward toward their respective Bristol Bay estuaries (Hartt, 1966). The recovery distribution of sockeye salmon (mostly .2-age mature fish) tagged in the Aleutian Island area in 1960 is illustrated in figure 14. Those approaching from far to the west apparently migrate rather directly toward the Bay. Recaptures by the high-seas fleet illustrate the course through the central Aleutian area. The lack of high-seas returns from releases in the eastern Aleutians (fig. 14D) indicates that this group must have turned northward and entered the Bering Sea before reaching lat. 175° W. Migration speed is rapid during the final 30 to 60 days at sea, averaging 25 to 30 miles (46.3 to 55.6 km.) per day.

Even as late as May 1, sockeye salmon from Bristol Bay are distributed over vast areas at sea extending from 1,200 miles (2,222 km.) to the west off the Kamchatka Peninsula to 1,200 miles to the east in the central Gulf of Alaska. Figure 15 illustrates the tagging areas during the period May 1 to June 15 from which Bristol Bay recoveries were subsequently received in the year of release.

The bulk of the run passes through the Aleutian Islands area between June 1 and 20, and through the estuaries between June 23 and July 18, with the peak between July 2 and 9. Tagging has indicated a sequential correspondence between date of

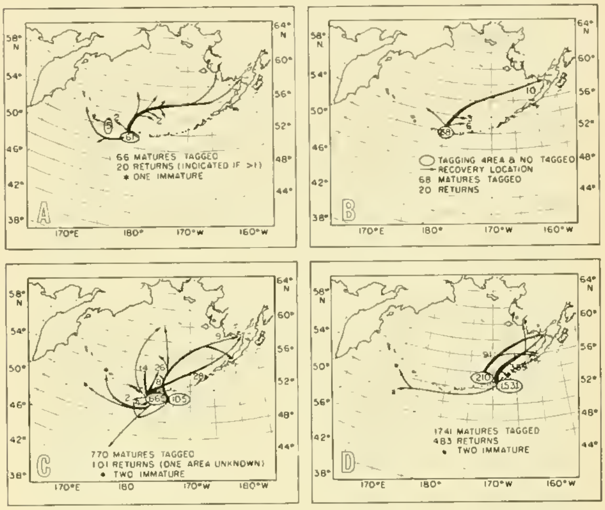

A
66 MATURES TAGGED
20 RETURNS (INDICATED IF >1)
* ONE IMMATURE
B
TAGGING AREA & NO TAGGED
RECOVERY LOCATION
68 MATURES TAGGED
20 RETURNS
C
770 MATURES TAGGED
101 RETURNS (ONE AREA UNKNOWN)
• TWO IMMATURE
D
1741 MATURES TAGGED
483 RETURNS
• TWO IMMATURE
170°E
180°
170°W
160°W

FIGURE 14.—Distribution of recoveries of sockeye salmon tagged and recovered in 1960 (U.S. tagging). Panels A, C, and D each show the results from two areas of operation; panel B shows the results from one.

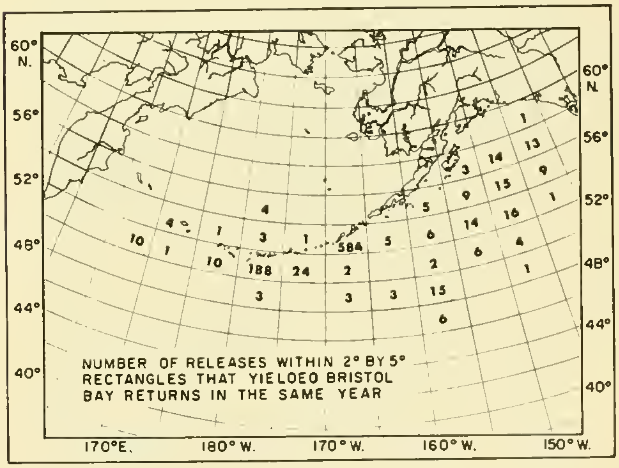

NUMBER OF RELEASES WITHIN 2° BY 5° RECTANGLES THAT YIELOEO BRISTOL BAY RETURNS IN THE SAME YEAR
170°E.
180° W.
170° W.
160° W.
150° W.
60° N.
56°
52°
48°
44°
40°

FIGURE 15.—Areas of release of sockeye salmon tagged between May 1 and June 15, and subsequently recovered in Bristol Bay in the same year between June 26 and July 24 (U.S. data 1956–65, Canadian data 1961–65, Japanese data 1958–61).

release in the Aleutians area and date of recovery in the commercial fishery and a tendency toward more rapid movement by the later migrants (Hartt, 1966). Many of the fish still feed actively on a variety of animals when within only 100 miles (185 km.) of the estuaries.

The immature .2-age fish during their third summer at sea follow a course similar to that of the .2-age mature fish except that they continue westward and northwestward in the Aleutian Islands and Bering Sea areas, rather than returning northeastward toward Bristol Bay (fig. 11D). They average 46 to 48 cm. long and are slimmer than the .2-age mature fish. Immature salmon begin to arrive in the Aleutian area just after the mature fish have passed and continue on a course similar to that described for their migrations in the previous summer as .1-age fish.

The earlier timing of the maturing group of .2-age fish indicates that they segregate from those not maturing, apparently by accelerating their speed or by taking a shorter route. As .1-age fish the previous summer they had been thoroughly mixed with the immature group, as verified by the fact that .1-age immature fish tagged in the same purse seine set frequently yield Bristol Bay returns both 1 year and 2 years later (Hartt, 1966).

The summer migrations of the .2-age immature sockeye salmon can be illustrated more completely by tag returns from U.S. tagging in 1964 (fig. 16). In 1964, substantial numbers of .2-age immature fish were tagged in the central Aleutian area and in the central Gulf of Alaska, so that together the tag returns bring out the salient features of migration. The 312 fish tagged south of Adak Island were released between late June and mid-August and were part of the characteristic summer migration that passes westward south of the Aleutian Islands. The 16 high-seas recoveries in 1964 (late July and early August) illustrate the westward and northwestward summer migration of immature fish into the western North Pacific and Bering Sea. The high-seas returns of mature fish in 1965 were probably en route to Bristol Bay, and the five Bristol Bay coastal returns together with a lack of coastal returns from areas other than Bristol Bay illustrate that fish migrating south of the Aleutians were primarily of Bristol Bay origin. The 404 fish tagged in the central Gulf (fig. 16) were released during May 1964, at which time the enclosed area was the apparent center of abundance of .2-age immature sockeye salmon as judged by longline sampling throughout the Gulf. The four coastal returns from Bristol Bay in 1965 demonstrate the presence of this stock and the nine Gulf coastal returns indicate a mixture of all major Gulf of Alaska stocks as well. The three high-seas returns in 1964 near the central Aleutians, all in late July and early August, show that part of the group from the central Gulf entered the mass westward migration south of the Aleutians. In all probability these fish were the Bristol Bay components of the Gulf mixture, and, thus, illustrate the summer return migration from the Gulf of at least some of the Bristol Bay immature fish. The route followed by the Gulf of Alaska stocks is not known, but they apparently did not enter the migration south of the central Aleutians, since tagging in that area yielded no Gulf coastal returns. Thus, the data in figure 16 illustrate that the migratory course of different salmon stocks can be discrete even though they overlap at certain times and places, which in turn suggests inherently different responses to whatever cues may be guiding them even at the immature stage.

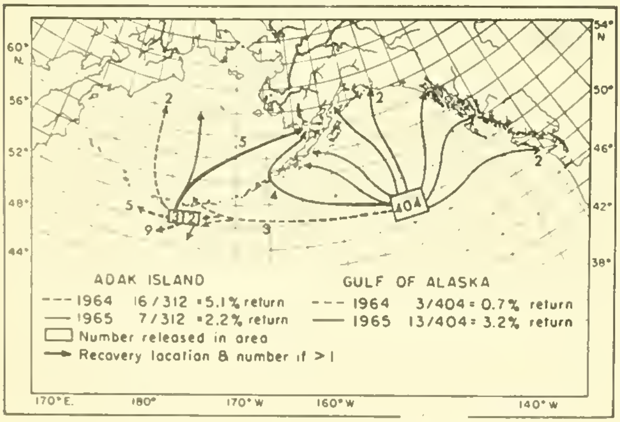

60° N.
56°
52°
48°
44°
54° N
50°
46°
42°
38°
170° E.
180°
170° W
160° W
140° W
2
5
5
9
312
3
4
404
2
2
ADAK ISLAND
--- 1964 16/312 = 5.1% return
— 1965 7/312 = 2.2% return
Number released in area
Recovery location & number if > 1
GULF OF ALASKA
--- 1964 3/404 = 0.7% return
— 1965 13/404 = 3.2% return

FIGURE 16.—Recovery distribution of sockeye salmon tagged as .2-age immature fish in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

The migrations of the .2-age immature sockeye salmon during the remainder of their third year at sea are apparently a repetition of those in their second year, i.e., westward or northwestward into the western North Pacific and Bering Sea during summer and fall, and then southward and eastward in the Subarctic Current in winter and spring (fig. 11E). During summer and fall they are mixed with the .1-age group of the next younger generation, and in winter they are joined by the newest generation of juveniles coming from Bristol Bay as discussed earlier. Finally, at the end of their third year and the beginning of their fourth summer, they again migrate westward in the Alaska Stream, northward through the Aleutian passes and northeastward to Bristol Bay. As .3-age mature fish they average 57 to 59 cm. in fork length and are accompanied by that part of the new .2-age group that is maturing in the same year. Their final migration is shown diagrammatically in figure 11F.

SUMMARY

A review of the entire ocean migration of Bristol Bay sockeye salmon as summarized in figure 17 indicates that they make two or three circuits of an elongated east-west course extending from about long. 165° E. to 140° W. The diagram is simplified and idealized. but it takes into account the major seasonal migrations and shifts in abundance shown by available catch and tagging data. The change in age is shown for convenience as occurring only at the western extremity of the migration, but undoubtedly each age group is distributed over a considerable part of the migratory path at the time the winter annuli are formed.

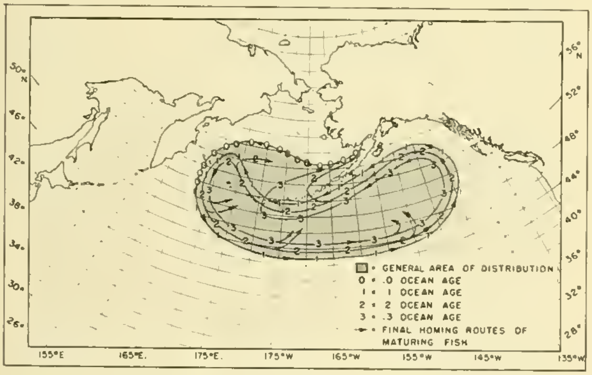


FIGURE 17.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on U.S. seine catch data, and on Canadian, Japanese, and U.S. tagging data through 1966.

COMMON CHARACTERISTICS OF SALMON MIGRATIONS

We have described the principal features of the migration of three of the major stocks of salmon in the North Pacific. We have postulated migrations and behavior that seem to us to be necessary if the salmon are to migrate to where they have been found, even though our information has some significant gaps. Many of the features of the migrations and behavior of these stocks are characteristic of most salmon stocks; we will summarize them in this section before we turn to a discussion of possible direction-finding or position-finding mechanisms.

The first outstanding feature is that each individual performs the migration once with no possibility of learning from a parent and with a poor chance of spawning successfully to perpetuate the race if it becomes lost or departs from the required time schedule. Clearly the navigational system is an entirely inherited series of responses to stimuli.

Second, the salmon migrate near the surface of the ocean, mostly in the upper 10 m. The success of the Japanese high-seas fishery, which uses surface gill nets (about 5 m. deep), and the research fishing experience with gill nets and longlines indicate that the salmon are typically caught near the surface. A few salmon (mostly chum salmon) have been taken by gill nets set at depths of 30 to 70 m. (International North Pacific Fisheries Commission, Annual Report, 1960: 26), but the latter depth seems to be near the depth limit. In coastal waters, coho salmon are often taken by trollers at a depth of 10 to 20 m. and chinook salmon between 20 and 30 m. (Milne, 1955).

The third outstanding feature is the long distance traveled. The pink salmon from southeastern Alaska or British Columbia and from the Karaginski district cover 3,000 miles (5,556 km.) or more in 12 to 15 months. Some of the pink salmon from the Karaginski district travel more than 4,000 miles (7,408 km.). Even greater distances are traveled by chum salmon which return to Hokkaido from south of Kodiak and chinook salmon which return to the Columbia River from south of the central Aleutian Islands. Further, the salmon that spend more than 1 year at sea, such as the chum and sockeye salmon, may well undertake an annual feeding migration in excess of 2,000 miles (3,704 km.). Our information about such migrations for immature fish is scanty, but the circumstantial evidence certainly indicates that the Bristol Bay sockeye salmon undertake substantial feeding migrations during their second and third summers at sea before they return to the home stream.

Fourth, much of the migration is not to and fro, but circular. The circuit which is closed only upon return home appears to consist of a single loop in the pink salmon from southeastern Alaska-British Columbia and Kamchatka and multiple loops in the Bristol Bay sockeye salmon. In none of these cases does it appear to be possible for the salmon to use memorized stimuli that could be followed back in reverse order.

During these long migrations the races that have been studied extensively occupy a distinctive but very large part of the ocean. Thus, the ranges of the various stocks of the several species overlap to an enormous extent. For example, tagged salmon have returned to Bristol Bay and also to the Fraser River from a group caught in a single set of the net in the northwestern part of the Gulf of Alaska. The salmon of the several species tagged near Adak Island, Alaska, have been recovered from nearly the western, northern, and eastern extremities of the range of Pacific salmon.

We believe that particular stocks of salmon have no tendency to school as a group in the ocean. We reinforce this assertion by the observation that usually we capture salmon of different species, age groups, and sizes on single sets of gear except when close to a destination of maturing salmon where a single stock may predominate. Even in such areas with a dominating single stock, the numbers caught per seine set are much more uniform over considerable areas and on successive days than would be true if the salmon were in separate, compact schools as are herring, for example.

Perhaps the most startling evidence of the individual behavior of salmon is indicated by the distribution of the mature Bristol Bay sockeye salmon in May and early June, 4 to 10 weeks before they arrive in Bristol Bay (fig. 15). At this time they are spread over some 2,000 miles (3,704 km.) of ocean in an east-west direction and some must migrate to Bristol Bay from as far as 1,200 miles (2,222 km.) away, either directly or in a dogleg to circumnavigate the Alaskan Peninsula. Within this range no evidence has appeared of segregation of the runs to the individual Bristol Bay rivers.

The salmon appear to be nearly continuous travelers. Many of them average about 10 miles (18.5 km.) per day while immature. When maturing, they commonly travel an average of 25 to 30 miles (46.3–55.6 km.) a day and occasionally may average more than 45 miles (83.3 km.) daily over long distances.

These speeds are clearly faster than most ocean currents that may carry the fish. The directional catches of the purse seine in many parts of the ocean for both mature and immature fish indicate clearly that the salmon exceed the speed of the current. The migration is positive, not a passive drifting.

These long migrations terminate on a remarkably consistent schedule. The migration of the Bristol Bay sockeye salmon past Adak Island (about 900 miles [1,667 km.] from home) is completed in about the same length of time and in about the same sequence of individuals as the migration through the fishing areas in Bristol Bay (Hartt, 1966). The runs in Bristol Bay in 1956–65 peaked on the average date of July 5, and the earliest and latest peaks were July 2 and July 9 (Royce, 1965). Eighty percent of the run in the same years arrived in 9 to 22 days. Other runs of salmon in more southerly latitudes commonly occur over greater periods of time, but we believe this spread is usually due to different schedules of the several populations that make up these runs. It appears to be common for a single interbreeding population to keep a schedule that varies from the average by only a few days.

The arrival of the salmon is less variable than the seasonal change in the weather. For example, average water temperatures at Weather Station P, located at lat. 50° N., long. 145° W. in the central Gulf of Alaska, show an average monthly increase of 2.2° C. from May to July (Bureau of Commercial Fisheries, 1957–65), but the range of attained mean monthly temperatures for 1957–65 shows that the May mean varied from 6.1° to 7.8° C., the June mean from 7.8° to 10.6° C., and the July mean from 10.6° to 13.3° C. If the timing of salmon migrations were governed by certain critical temperatures in the waters through which they are distributed, then the arrival date would vary by about 2 weeks around a mean.

The routes followed during the migrations seem unrelated to land or continental shelves. Sometimes a considerable concentration of salmon appears in passes and near points, but the normal migratory routes seem to be across open water, even where, as in the approaches to inner Bristol Bay, it would be convenient to follow close to the shore.

The remarkable directness of the final migration in the open sea is illustrated by the Karaginski district pink salmon that migrate through the area of the Japanese high-seas fishery. When the fish have been tagged and released from different points along a north-south line, the recaptures show the tendency to proceed rather directly toward their destination (fig. 8). Obviously, their migration is not random as suggested by Saila and Shappy (1963).

Many of the migration routes traverse different ocean domains. The Karaginski pink salmon, for example, within 2 months apparently travel from the eastwardly flowing central Subarctic Current across the Alaskan Gyre, across the westerly flowing Alaskan Stream, and through the Bering Sea Gyre in the western Subarctic Domain (see Dodimead et al., 1963:167). Bristol Bay sockeye salmon regularly occupy the Alaskan Gyre and the western Subarctic Gyre in late spring and migrate through the Bering Sea Gyre on the homeward migration. Such routes clearly take the salmon through parts of the ocean far removed from any recent mixing with home-stream waters, and we conclude, as does Neave (1964), that the olfactory sense cannot provide a significant source of guidance information except at the end of the route.

Much of this migration takes place through and during some of the most prolonged and violent ocean storms in the world. The weather of the Aleutians area (U.S. Department of Commerce, 1955: 343) is characterized by persistently overcast skies, high winds, and violent storms. No other oceanic area in the world is recognized as having worse weather in general than that of the Aleutian Islands—clear weather over large areas is rare. Even in the milder summer periods, the sky is obscured by fog, mist, haze, or clouds most of the time. In the outer parts of Bristol Bay (U.S. Department of Commerce, 1955: 631) the average weather in June (the month when most salmon are homeward bound) is 44 percent fog, mist, or haze, and mean cloud cover is 8/10. In the central Gulf of Alaska (U.S. Department of Commerce, 1955: 619) the average June weather is 25 percent fog, mist, or haze; the mean cloud cover is 9/10. Our own experience with several years of vessel operation in this area indicates that it is impossible to navigate by celestial observations alone, and we suggest that salmon have far too little opportunity to observe the direction of either the sun or the polarization of light to keep the kind of schedule that they manage.

POSSIBLE GUIDANCE MECHANISMS

Little can be said about the physiology of salmon which specifically explains how they navigate during transoceanic migrations, because the necessary experiments have not been performed. If certain generalizations are made, however, some interesting possibilities emerge from the migration data just presented and from the literature of fish physiology as a whole.

Two of the preceding generalizations from the tagging and seining data seem particularly significant. First, the most common direction of travel follows the various North Pacific currents. Second, salmon in the open sea do not drift with the current, but actively swim with it. We, therefore, conclude that the migrations of salmon on the high seas are actively directional in a way which somehow relates to the ocean currents. Directional cues for animal orientation have included celestial bodies, water movement, olfactory stimuli, and electrical or magnetic fields. Let us examine whether any of these are compatible with our data on salmon migrations.

SUN ORIENTATION

The sun, a prominent object by which some terrestrial animals navigate, could similarly serve salmon on the high seas. Indeed, certain lake fish have such an orienting mechanism (Hasler and Schwassmann, 1960). Also, some arthropods orient to the plane of polarization of sunlight (Ivanoff and Waterman, 1958). Arthropods and fish both require good visibility of the sun, however, because both become disoriented when clouds obscure the sun (Waterman, 1959; Hasler et al., 1958). Salmon, on the other hand, migrate at night as well as during the day and through regions where clouds obscure the sun almost continuously.

Furthermore, small lakes have only minimal amounts of wave action to complicate a fish's view of the sun, but marine fish must view the sun through a water surface which is never completely calm. Also, lake fish can migrate in straight lines: salmon migrate along circular as well as straight routes. This circumstantial evidence casts doubt on sun orientation as a primary navigational mechanism for Pacific salmon.

Although the cloudy weather of the North Pacific severely limits the possible use of sun orientation by salmon, use of the sun cannot be entirely eliminated from consideration. An oceanic bird, the slenderbilled shearwater (*Puffinus tenuirostris*), which makes an annual circum-Pacific, transequatorial migration, travels near the Aleutian Islands at about the same time that some salmon there begin their final homeward migration. The slenderbilled shearwater appears to use sun orientation as its primary navigational cue (Serventy, 1963), even though a related shearwater becomes disoriented during overcast conditions (Matthews, 1964). Despite such evidence on possible use of the sun, a simpler hypothesis to explain navigation by salmon on the high seas seems preferable.

ORIENTATION TO WATER MOVEMENT

Fish in rivers and streams are very sensitive to current direction and usually orient upstream to maintain position. Salmon smolts often show an active downstream orientation during their seaward migration. Optical, tactile, and lateral-line senses all seem to be involved in these rheotropisms, but the need for some kind of stationary reference point, such as a shore or the stream bottom, makes this an unlikely mechanism for use on the high seas where reference points are very distant. Direct detection of water movement also seems unlikely because of the very large size of the water bodies and, therefore, the correspondingly slight velocity gradients. A gradient does exist, however, and the sensitivity of fish to velocity gradients in the absence of other cues appears untested; it cannot be entirely excluded as a possible navigational mechanism.

Salmon are perhaps capable of detecting the interfaces between moving bodies of water either through sensing of chemical differences between two bodies of water or by detecting the water turbulence at the interface. This navigational cue would lead to a great deal of random swimming, however, while the fish searches for these margins and would tend to concentrate fish near the margins of ocean currents; neither behavior is characteristic of salmon migration. Salmon are relatively evenly distributed across the ocean currents and the migration routes appear well defined and "purposive," often converging on the spawning streams from several directions.

ELECTRICAL POTENTIALS AVAILABLE FOR ORIENTATION

Because sea water is an electrical conductor moving through the earth's magnetic field, the production of an electrical voltage can be expected. Oceanographers have recognized the electrical potential of sea water for some time. Stommel (1954) found potential differences of 0.2 to 2.6 v. across long distances in the Atlantic Ocean among several submarine cables. Similar voltages were observed between Florida and Cuba. Snyder (1966), in describing the underwater search for the atomic submarine *Thresher*, reported a voltage of about 140 mv. (millivolts) between towed electrodes, one on the surface and one in about 2,440 m. of water. Hughes (1962) attempted to use these voltages to measure ocean currents by towing electrodes, spaced 46 m. apart, behind a ship. He found voltages of 3 to 5 mv. when the ship crossed the current and a reversal of polarity when the ship traveled in the reverse direction. Voltage was nil when the ship moved either with or against the current. The voltages per knot of current varied considerably in shallow water but consistency was greater in deep water.

The electrical gradient that might be available for navigational use, therefore, is about 0.1 to 0.5 μv. (microvolts)/cm. Because these voltages are directly related to the current and are polarized with respect to its direction, electrical cues seem to be a possible navigational device for salmon on the high seas. Magnetic sensitivity has been shown for several animals, but the receptor organ is unknown. Presumably, detection occurs as a result of a voltage induced within the receptor (Brown, Barnwell, and Webb, 1964). The basic question, therefore, is whether fish can detect minute voltages.

ELECTRICAL SENSITIVITY OF FISH

At present no information appears to be available on the electrical sensitivity of salmonids. Even though experiments in the electrical guidance of salmon smolts migrating downstream have been large and intensive, this work seems not to have included any examination of possible electroreceptor organs. Certain other fish, however, which have electric organs as well as electrical receptors have been investigated extensively.

One group of electric fish includes the electric eel. Hagiwara, Szabo, and Enger (1965a) described the physiological properties of electroreceptors in the electric eel, *Electrophorus*. Two types of electroreceptors reside in the lateral line. Some of them respond only to electrical stimuli, but others are mechanically and electrically sensitive. The threshold of the "pure" electroreceptors to imposed square pulses was 2 to 30 mv./cm. and the discrimination threshold was 1.5 to 5 mv./cm. Since the electric eel's low-voltage pulses that it uses for electrolocation are still relatively high voltages—20 to 50 v.—Hagiwara et al. (1965a) suggested that the response of the mechanoreceptors to these electric signals may be only incidental and not biologically significant. Because salmon hardly experience signals of this magnitude, however, more useful interpretations can be gained from information on a group of weakly electric fish.

Members of several genera of the weakly electric gymnotid eels have electric organs that produce electrical pulses of about 30 mv. at 40 to 600 per second. Lissmann (1951) recorded such signals from *Gymnarchus* and played back the fish's own signals through a pair of electrodes in the water at a distance from the fish. At a strength of about 30 μv. the fish responded to the signals by immediately attacking the electrodes. Lissmann and Machin (1958) performed behavioral experiments with *Gymnarchus* which indicated that the fish discriminated changes in the electrical field of 0.02 μv./cm.

In contrast, the sensitivity of individual receptors is much less than that indicated by behavioral experiments. Hagiwara and Morita (1963), who recorded electrical activity from individual neurons of the lateral-line nerve in two other gymnotids, *Staetogenes* and *Gymnotus*, found a threshold for an imposed electrical field of about 10 mv./cm. along the long axis and a discrimination threshold of 0.1 to 1 mv./cm. Hagiwara et al. (1965b) found that the electroreceptors of *Sternarchus* responded phasically and tonically to stimuli. The rate of response was highest in the presence of a metal conductor and lowest in the presence of a plastic plate over the receptor. When an electrical field was applied between head and tail, response rate changed for different polarities. At the site of greatest electrical sensitivity they found only one kind of sensory organ. The organ included several cells grouped around a single opening on the lateral line and innervated by a single sensory nerve fiber.

Enger and Szabo (1965), who recorded electrical activity in the medulla of several gymnotids, concluded that tonic responses can yield information to the fish about the presence and position of objects within the electric field and that phasic responses give information on movement, direction of movement, the size of an object, and the position of the front edge of that object. Dijkgraaf (1963) described the electrical sensitivity of the gymnotid group as about 0.05 μv./cm. or 0.05 μamps. (microamperes). Machin (1962) concluded that such small signals could be distinguished from background "noise" if about 40,000 receptors were involved and that this was a reasonable number of electroreceptors which might occur in the lateral-line system. Thus, it appears reasonable to conclude that at least some fish possess electroreceptors of adequate sensitivity to detect and determine the polarity of electrical voltages of the magnitude produced by ocean currents.

PREDICTION OF ELECTRICAL SENSITIVITY FOR SALMON

As indicated above, no investigations are known concerning the electrical sensitivity of adult salmon or of the presence of receptor organs in the lateral line of salmon which might be electrically sensitive. In his recent review of lateral-line function, however, Dijkgraaf (1963) came to several conclusions that might apply to salmon. His first suggestion was that the basic electroreceptor organ is a modified mechanoreceptor which has achieved maximal response to electrical stimuli. Secondly, because electrical receptors occur in the lateral line of several widely separated groups of fish, he suggested that they may have evolved independently several times. It would appear that any fish that has lateral-line organs possessing even secondary electrical sensitivity could develop an electronavigation system relatively easily and quickly. For example, the galvanotropism of the catfish *Parasilurus* (Abe, 1935) seems to be such a development. Although we have no physiological information to confirm electronavigation on the high seas for salmon, the circumstantial evidence described above indicates that it should be included among the more likely sensory mechanisms that salmon may use during their travels.

CONCLUSIONS ON GUIDANCE MECHANISMS

We believe that the salmons' migration cannot be performed if they migrate or drift at random, or if they depend on any memorized visual or olfactory cues at any time except during the final location of the home estuary and stream. We note that the salmon predominantly travel actively with the ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. We note also that ocean currents produce electric potentials in a range which some fish can detect. We suggest, therefore, that salmon may depend on electromagnetic cues from ocean currents. We suggest further that their response to all migatory cues is inherited, not memorized.

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HYDROLOGICAL AND BIOLOGICAL CHARACTERISTICS OF FLORIDA'S WEST COAST TRIBUTARIES[1]

By Alexander Dragovich,[2] John A. Kelly, Jr.,[3] and H. Grant Goodell[4]

ABSTRACT

Data are given for 10 stations in the Hillsborough, Alafia, Little Manatee, Manatee, Myakka, Peace, and Caloosahatchee Rivers, which flow into west Florida bays. Variations in temperature, salinity, chlorophyll "a," dissolved oxygen, total phosphorus, inorganic phosphate-phosphorus, copper, and iron were recorded over a 13-month period. The variations are discussed in terms of differences in precipitation, river discharges, and general geological properties of river basins. Certain hydrological conditions of the tributaries are compared with the conditions of the adjacent neritic waters of the Gulf of Mexico.

Thermal differences between surface and bottom were negligible. The temporal distribution of salinity was influenced by precipitation. Distribution of total phosphorus and inorganic phosphate-phosphorus was related to the underlying phosphatic formations of the various river basins. Maximum values of total dissolved oxygen occurred in winter and minimum in summer; no anaerobic conditions were encountered. Concentrations of chlorophyll "a," copper, and iron were higher in the rivers than in the adjacent sea.

The quantity of nutrients contributed by rivers to the sea is determined largely by the volume of river flow, not by the actual concentrations of the nutrients. The possible relation between the mean input of various materials by the tributaries, and the presence of the Florida red-tide organism, *Gymnodinium breve* Davis, was tested. A correlation between iron and *G. breve* was significant at the 80-percent level.

Ecological studies were made of the waters of Tampa Bay, Charlotte Harbor, and the adjacent Gulf of Mexico as part of an investigation of the Florida red-tide organism, *Gymnodinium breve*. Red tide in waters along the southwest Florida coast is associated with dense concentrations of *G. breve*, discolored water, and fish kills.

Red tides throughout the world occur primarily in coastal areas and usually in periods of heavy rainfall and increased river discharge. The presence and growth of phytoplankton in coastal waters depend largely on the quantity and quality of inorganic and organic nutrients, particularly trace metals and external metabolites (Provasoli, 1958).

Rivers make annual additions of nutrients to the sea. In evaluating the effects of Florida west coast tributaries on red-tide outbreaks and estuarine productivity, a thorough knowledge of the hydrology of the tributaries may be helpful. Because published information on the hydrology of these streams is limited, a survey was undertaken to assess hydrological characteristics of seven major rivers that flow into Gulf estuaries. Dragovich and May (1962) listed publications concerned with the hydrology of streams of the west coast of Florida.

We studied monthly variations in certain hydrological and biological properties of the Myakka, Peace, and Caloosahatchee Rivers which enter the Charlotte Harbor estuarine system. These streams were selected because of their importance to red-tide problems and coastal oceanography. The Hillsborough, Alafia, Little Manatee, and Manatee Rivers, which are tributaries of Tampa Bay, were included because new ecological factors were added to those measured

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in previous studies (Dragovich and May, 1962).

Temperature, salinity, chlorophyll "a," oxygen, total phosphorus, inorganic phosphate-phosphorus, copper, and iron were measured.

Copper was included in our past studies and in the present one because its high toxicity to laboratory cultures of *G. breve* suggested that it might be a limiting factor in the physiology of this species in natural waters. It was determined only in the Myakka, Peace, and Caloosahatchee Rivers because earlier studies in Tampa Bay tributaries revealed that the concentrations there were nontoxic to *G. breve* (Dragovich and May, 1962).

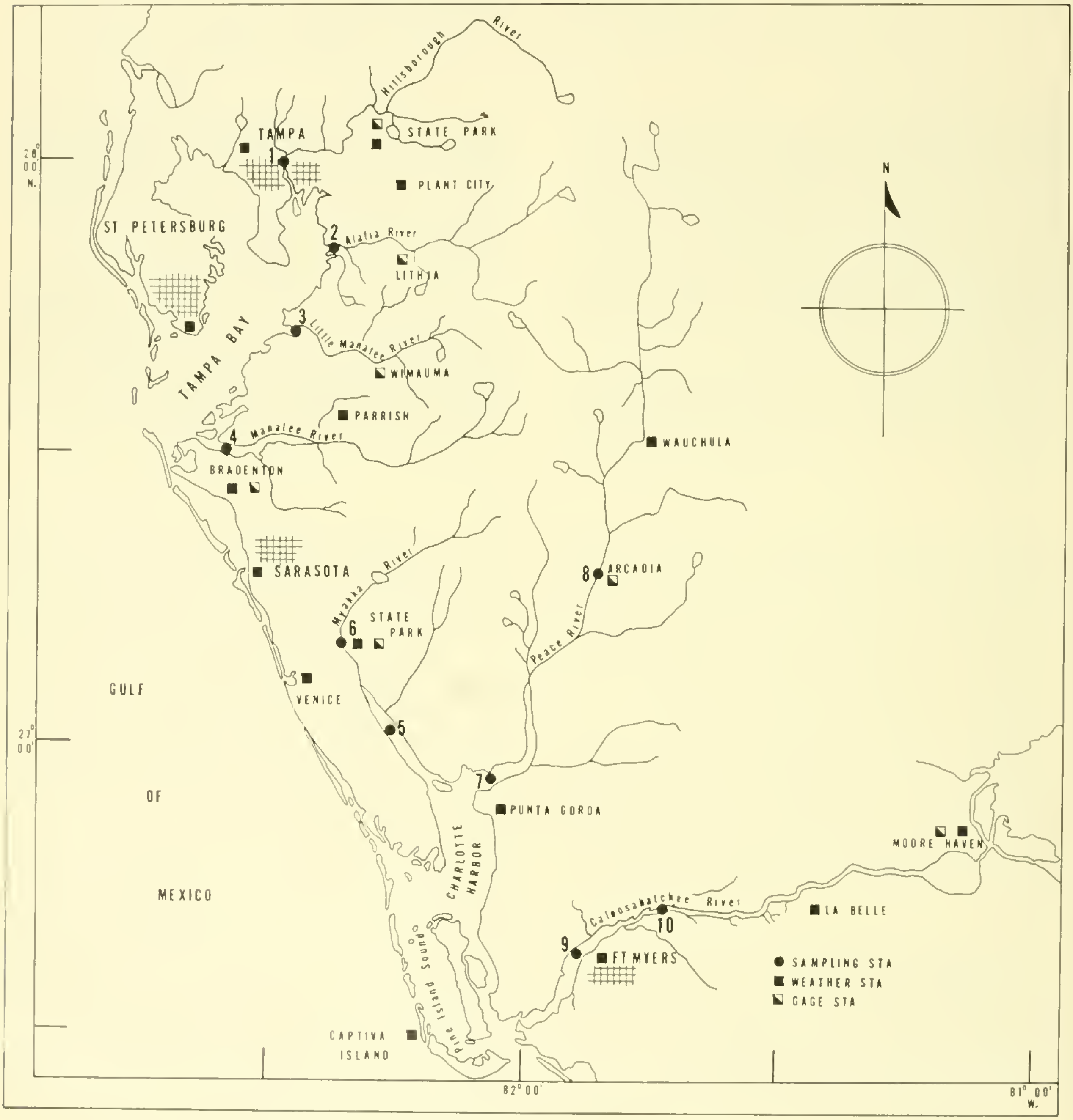
Hillsborough River
TAMPA
1
STATE PARK
PLANT CITY
28° 00' N.
N
ST PETERSBURG
2
Alafia River
LITHIA
TAMPA BAY
3
Little Manatee River
WIMAUMA
PARRISH
4
Manatee River
BRADENTON
WAUCHULA
SARASOTA
Myakka River
8
ARCADIA
6
STATE PARK
Peace River
GULF
OF
MEXICO
VENICE
27° 00'
5
7
PUNTA GORDA
CHARLOTTE HARBOR
MOORE HAVEN
Caloosahatchee River
10
LA BELLE
9
FT MYERS
Pine Island Sound
● SAMPLING STA
■ WEATHER STA
◩ GAGE STA
CAPTIVA ISLAND
82° 00'
81° 00' W.

FIGURE 1.—West coast of Florida showing rivers, sampling locations, and weather and gage stations.

SAMPLING PROCEDURES AND LABORATORY TECHNIQUES

The study began in January 1964 and continued through January 1965. The sampling consisted of monthly collections of water samples near the surface and bottom at 10 stations (fig. 1). Station depths ranged from 1.8 to 4.6 m. Water samples at all stations were collected with a modified Van Dorn sampler (Van Dorn, 1957). Samples for total phosphorus and inorganic phosphate-phosphorus were immediately put into 200-mm. culture vials capped with polyethylene-lined screw-caps, and quick-frozen. Samples for the determination of copper and oxygen were transferred into 250-ml. glass-stoppered bottles, and for salinity into 113-ml. prescription bottles. Water samples for the determination of iron and chlorophyll were placed in polyethylene containers and sterile 500-ml. Erlenmeyer flasks.

The following physical and chemical methods of analysis were employed:

Water temperature—mercury thermometer calibrated to the nearest 0.1° C.

Salinity—Mohr-Knudsen method (Knudsen, 1901).

Inorganic phosphate-phosphorus—Robinson and Thompson (1948) method.

Total phosphorus—Harvey (1948) method.

Total dissolved copper—Hoste, Eeckhout, and Gillis (1953) method.

Total iron—Armstrong (1957) method.

Dissolved oxygen—Winkler method (Jacobsen, Robinson, and Thompson, 1950).

Chlorophyll "a"—Richards and Thompson (1952) method.

Samples for copper analysis were filtered, but not those for total phosphorus and iron. The iron and total phosphorus values represent the respective elements in true solution and particulate form combined.

DISTRIBUTION OF METEOROLOGICAL, HYDROLOGICAL, AND BIOLOGICAL PROPERTIES

PRECIPITATION

Data on precipitation are from the Annual Summary of Climatological Data, 1964, prepared by the Environmental Science Services Administration, U.S. Department of Commerce. Stations used were: Tampa, Hillsborough River State Park, and Plant City for the Hillsborough and Alafia Rivers; St. Petersburg, Parrish, and Bradenton for the Little Manatee and Manatee Rivers; Sarasota, Venice, and Myakka for the Myakka River; Wauchula and Punta Gorda for the Peace River; and Captiva Island, Fort Myers, La Belle, and Moore Haven for the Caloosahatchee River (fig. 1).

From January 1964 to January 1965 the mean annual precipitation was 135.1 cm. for Tampa Bay and 108.2 cm. for the Charlotte Harbor-Pine Island Sound area. The period July through September contributed 54 percent and February 10.5 percent of the total precipitation. Minimum and maximum mean monthly precipitation values were 6.6 cm. and 267.5 cm. in the area of the Hillsborough and Alafia Rivers.

RIVER DISCHARGE

The office of the U.S. Geological Survey, Branch of Surface Water, Ocala, Fla., supplied information on river discharges at seven stations (fig. 1). These stations gave a combined flow of 2,566,729,830 m.^{3} from all rivers from January 1964 through January 1965 (grand total discharged). Volumes of water were highest in the Hillsborough and Peace Rivers (figs. 2, 8, and 9). River flow was highest in periods of heavy rainfall (figs. 2–11).

SALINITY

Only two stations (6 and 8) possessed limnetic characteristics throughout the period of study. Salinities at the remaining stations ranged from 0.12 p.p.t. (parts per thousand) at stations 9 and 1 during the rainy season to 28.93 p.p.t. at station 4 in May just before the onset of the rainy season.

The true temporal and vertical distribution of salinity cannot be assessed from these observations because the samples were collected without regard to tidal stage. Nevertheless, the rainfall-river discharges and salinity showed a close inverse relation (figs. 2, 4, 6, and 11). At a few stations (1, 5, and 10) salinity reached 0.12 p.p.t. during, or immediately following, periods of heavy rainfall.

The difference in salinity between the surface and bottom at all stations varied from 0 to 13.11 p.p.t. Vertical mixing was relatively good at stations 4, 5, 7, 9, and 10. The most pronounced vertical differences of salinity were at stations 1, 2, and 3, near the mouths of the Hillsborough, Alafia, and Little Manatee Rivers.

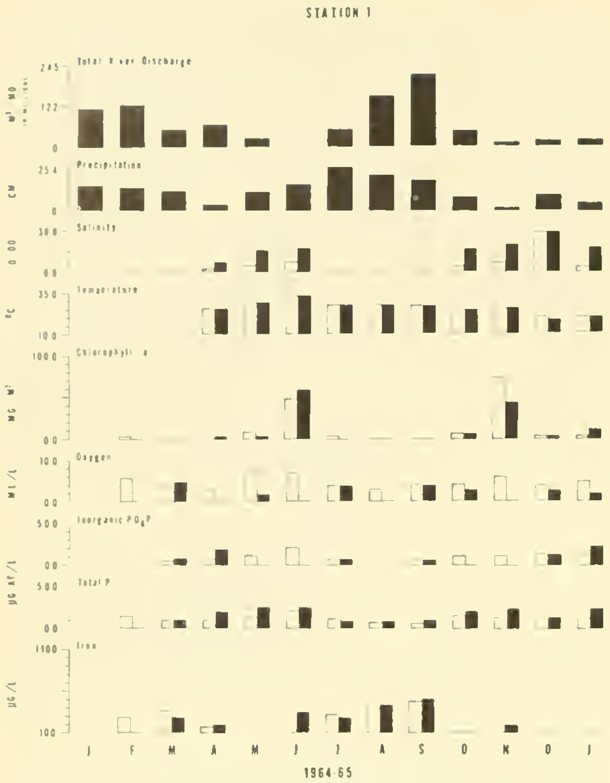

FIGURE 2.—River discharge, precipitation, and hydrological properties at station 1, Hillsborough River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

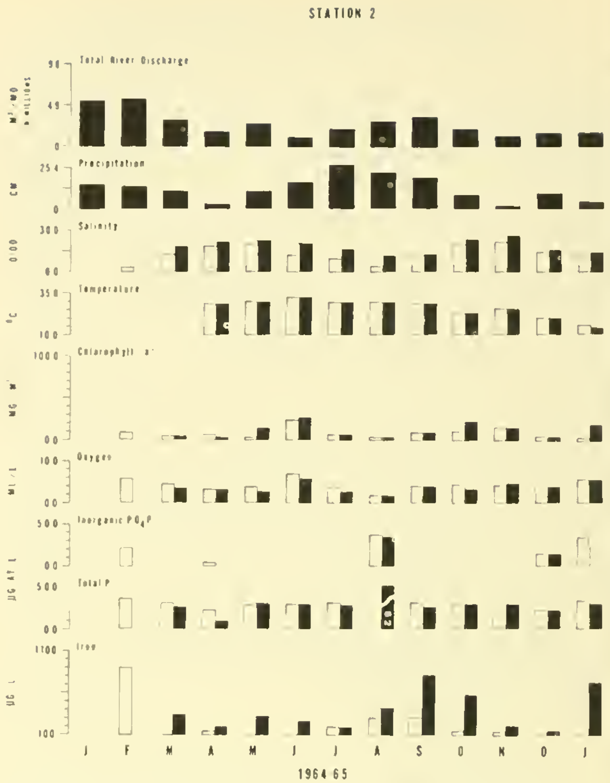

FIGURE 3.—River discharge, precipitation, and hydrological properties at station 2, Alafia River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

Salinity is a limiting factor in the distribution of many marine and estuarine organisms, but reliable data on the relation of estuarine organisms to salinity are scarce (Gunter, 1961). The unstable salinity at most stations was an ecological barrier to stenohaline and to some euryhaline organisms. Conditions were suitable only to forms that can exist over the entire salinity range from fresh water to sea water.

Since the favorable salinity range for the growth of *Gymnodinium breve* lies between 21 and 37 p.p.t. (Rounsefell and Dragovich, 1966), salinities at the river stations were seldom favorable for its growth.

TEMPERATURE

The annual temperature ranges during this study were the observed tolerance ranges for fishes (Springer and Woodburn, 1960) and invertebrates (Dragovich and Kelly, 1964) in Tampa Bay and for resident biota in Florida Bay (Tabb and Manning, 1961).

The water temperature varied from 12.8° to 32.4° C.; monthly changes in all rivers and stations were similar (figs. 2–11). Temperatures were high from April through September (highest in June and July 1964), and low in December, January, and February (lowest in January 1965).

Temperature differences between surface and bottom were less than 0.5° C. in about 92 percent of the observations; twice they exceeded 1° C. Temperatures at the stations with brackish water were affected by displacement of water masses during tidal oscillations.

CHLOROPHYLL "a"

Concentrations of chlorophyll "a" varied from 1.3 to 245.5 mg. per cubic meter. The highest individual and mean values for the entire period were at station 8 in the Peace River (fig. 9), where mean surface and bottom concentrations were 82.3 and 49.2 mg. per cubic meter. At other stations, corresponding values varied from 3.9 to

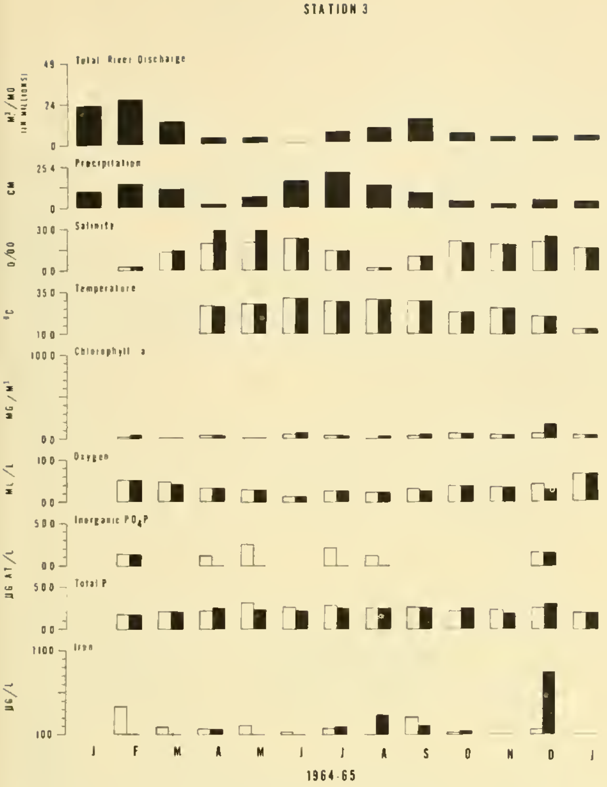

Figure 4.—River discharge, precipitation, and hydrological properties at station 3, Little Manatee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

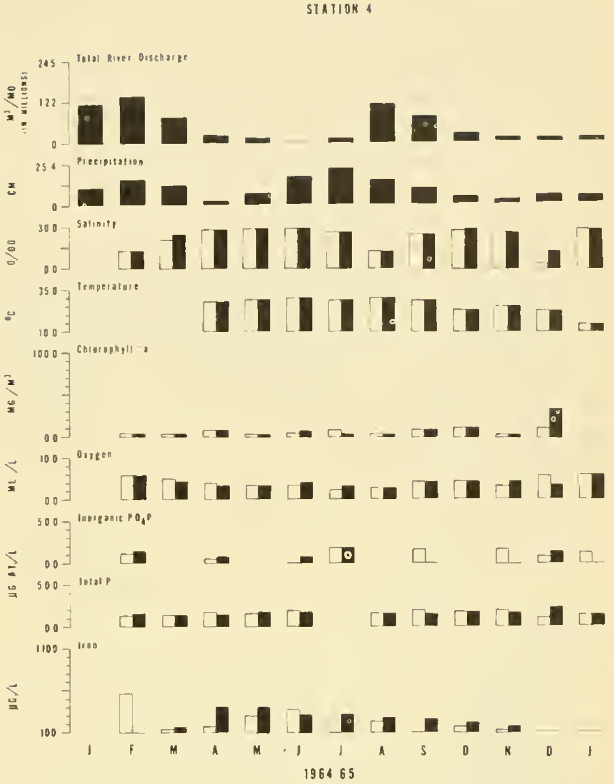

Figure 5.—River discharge, precipitation, and hydrological properties at station 4, Manatee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

17.9 mg. per cubic meter; in 74 percent of the observations they were below 10 mg. per cubic meter.

The temporal distribution of chlorophyll "a" was dissimilar between stations (figs. 2–11). The expected peaks during phytoplankton blooms in the spring or fall did not appear at all stations. The production was lowest in February, March, May, July, and August 1964 and in January 1965.

Concentrations of chlorophyll "a" at all river stations were higher than the corresponding values in the adjacent Gulf of Mexico (table 1). The extremely high means for surface and bottom at the upstream station in the Peace River were 30.2 and 17.8 times greater than the corresponding values from the upper section of Charlotte Harbor. The mean surface concentration of chlorophyll "a" at this river station was comparable to the maximum reported from East Lagoon, Galveston, Tex., and higher than the mean values reported from Alligator Harbor and the Dry Tortugas, Fla. (table 2).

The mean values of chlorophyll "a" in Tampa Bay tributaries were highest in the Hillsborough and Alafia Rivers (table 1). Except for the Hillsborough River, the mean chlorophyll "a" values in Tampa Bay tributaries were similar to those in upper Tampa Bay but lower than those from East Lagoon, Tex., and Alligator Harbor, Fla. (table 2).

The dissimilarity among stations in production of chlorophyll "a" may have been caused by a combination of factors. Zein-Eldin (1961) attributed the vertical gradient of chlorophyll "a" in East Lagoon to tidal oscillations and turbulence. The fact that mean concentrations were lower at the river mouths of the Hillsborough, Alafia, and Little Manatee Rivers than in Hillsborough Bay favors this view.

PRODUCTION OF ORGANIC MATTER

The rate of organic production in tributaries was estimated from the following equation (Ryther and Yentsch, 1957):

$$P=\frac{R}{K}\times C\times 3.7$$

TABLE 1.—*Mean concentrations of chlorophyll "a," iron, and inorganic phosphate-phosphorus in Florida west coast tributaries and adjacent bays and neritic waters of the Gulf of Mexico, January 1964 to January 1965*

[S=surface; B=bottom]

Location	Chlorophyll "a"		Iron		PO_4-P	
	S	B	S	B	S	B
Tampa Bay area	*mg./m.³*	*mg./m.³*	*µg./l.*	*µg./l.*	*µg. at./l.*	*µg. at./l.*
Rivers:						
Hillsborough	12.41	12.03	202.4	235.0	9.6	19.1
Alafia	8.13	12.04	216.6	381.0	33.6	29.1
Little Manatee	3.92	5.05	187.5	219.0	22.2	24.8
Manatee	5.44	7.68	217.0	251.6	15.1	16.6
Bays:						
Old Tampa Bay	5.56	9.40	115.0		23.2	25.8
Hillsborough Bay	30.22	19.47	147.8		24.4	24.0
Upper Tampa Bay	6.78	7.37	74.1		22.2	24.0
Lower Tampa Bay	3.14	3.37	40.6		14.5	16.4
Gulf:						
9.3 km. off Tampa Bay	1.17	1.03	16.3	19.4	2.6	3.2
18.5 km. off Tampa Bay	3.78	0.95			1.4	0.0
27.8 km. off Tampa Bay	0.50	.54			0.6	1.8
37.1 km. off Tampa Bay	.36	.58	6.0	5.3	.4	.6
Charlotte Harbor area						
Rivers:						
Myakka:						
Station 6	7.18	6.76	622.9	683.0	9.6	7.1
Station 5	5.25	5.79	299.2	434.3	6.3	7.2
Peace:						
Station 8	82.28	49.93	460.6	490.4	32.6	30.7
Station 7	8.74	9.89	329.7	305.9	18.6	18.4
Caloosahatchee:						
Station 10	10.65	13.53	265.8	535.5	2.4	4.4
Station 9	12.13	17.94	320.9	414.3	6.2	6.4
Bays:						
Upper Charlotte Harbor	2.73	2.80	111.9	111.6	11.5	9.3
Lower Charlotte Harbor	2.37	2.28	93.3	76.4	10.4	5.8
Gulf:						
9.3 km. off Boca Grande	1.86	1.28	26.0	20.3	1.6	1.1
18.5 km. off Boca Grande	.95	.53			.7	1.0
27.8 km. off Boca Grande	.54	.42		-	1.0	.7
37.1 km. off Boca Grande	.28	.29	16.5	4.6	.7	.6

TABLE 2.—*Reported concentrations of chlorophyll "a" in coastal and marine areas of the Atlantic Ocean and the Gulf of Mexico*

Location	Concentration		Reference
	Mean	Maximum	
	mg./m.³	*mg./m.³*	
East Lagoon, Galveston, Tex	17.6	84.6	Zein-Eldin (1961).
Alligator Harbor, Fla	4.3	14.0	Marshall (1956).
Florida coastal waters[1]		30.7	Marshall (1956).
Dry Tortugas, Fla	0.3	--	Riley (1938).
North Atlantic	----	2.5–3.6	Riley (1939).

[1] This value was observed in the midst of bloom of *Gymnodinium breve*.

where P is the productivity rate in grams of carbon per square meter per day, R is the radiation factor found from the graphs of Ryther and Yentsch (1957), K is the extinction coefficient of the water, and C is grams of chlorophyll "a" per cubic meter. Because the derived carbon quantities are based primarily on chlorophyll values, their relative values and temporal and areal distribution resemble those of chlorophyll "a." The mean approximations of organic production exceed the analogous values (0.27 g. per square meter per day) from East Lagoon, Tex. (table 2).

The rivers contributed a substantial quantity of organic matter to the adjacent sea (table 3). Included are endocrine products liberated in the process of chlorophyll synthesis (Provasoli, 1958). The fate of these metabolites is not known, but they may have a bearing on the genesis of phytoplankton blooms and particularly of Florida red tide, if only a fraction reaches the bays and the adjacent sea. From the chlorophyll data and the river discharges, it may be deduced that quantitatively more metabolites reach the bays and adjacent sea during heavy rainfall than in periods of light rainfall.

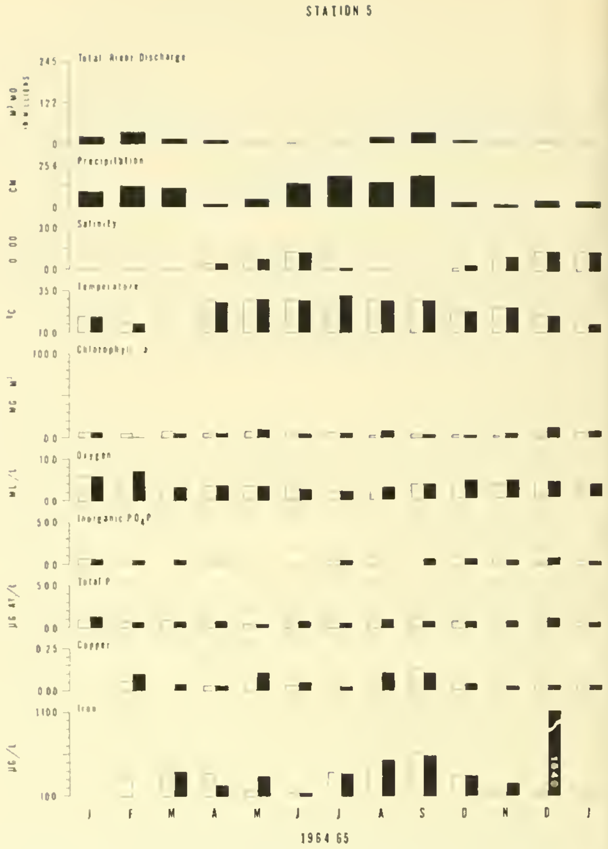

FIGURE 6.—River discharge, precipitation, and hydrological properties at station 5, Myakka River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

TABLE 3.—*Mean estimates of primary productivity (g. C/m.^{2}/day) in west Florida rivers*

River	1964												1965	Average
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	
Hillsborough:														
Station 1	------	0.23	0.38	0.42	1.25	9.70	0.32	0.19	0.29	0.87	7.97	0.39	1.05	1.92
Alafia:														
Station 2	------	.16	1.45	1.44	2.95	9.53	1.63	1.15	2.69	4.13	3.24	.67	2.61	2.63
Little Manatee:														
Station 3	------	.49	.59	.83	0.44	1.10	.68	.38	.69	.91	0.67	1.40	0.39	0.71
Manatee:														
Station 4	------	.22	.45	.95	.38	0.69	.62	.48	.97	1.10	.39	1.92	.12	.69
Myakka:														
Station 5	0.90	.57	1.19	1.05	1.58	.64	.74	.93	.46	.46	.55	1.18	1.18	.87
Station 6	.39	.84	.51	2.00	1.03	1.81	1.10	1.41	.33	.59	.66	.37	.27	.87
Peace:														
Station 7	1.49	2.33	.79	1.54	1.21	1.34	1.54	2.91	.56	1.12	1.42	1.89	.64	1.44
Station 8	8.36	4.29	3.25	2.84	3.26	3.57	2.42	4.13	1.30	25.14	24.58	8.26	4.77	7.39
Caloosahatchee:														
Station 9	2.42	8.40	3.40	1.02	1.27	1.04	1.26	1.95	1.08	4.67	.97	1.55	.98	2.28
Station 10	1.95	1.32	2.74	2.37	.68	1.22	1.67	1.49	.71	4.79	1.29	3.06	1.31	1.89

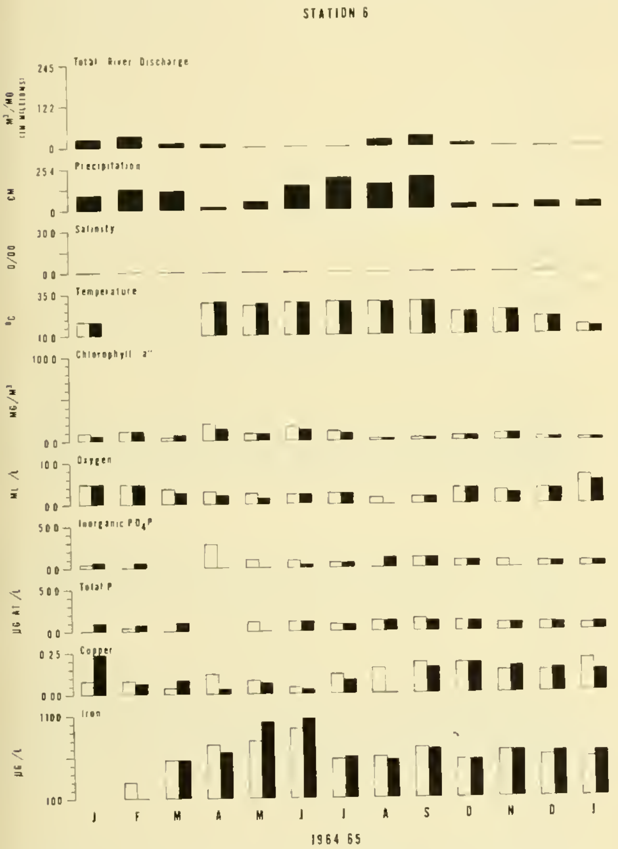

FIGURE 7.—River discharge, precipitation, and hydrological properties at station 6, Myakka River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

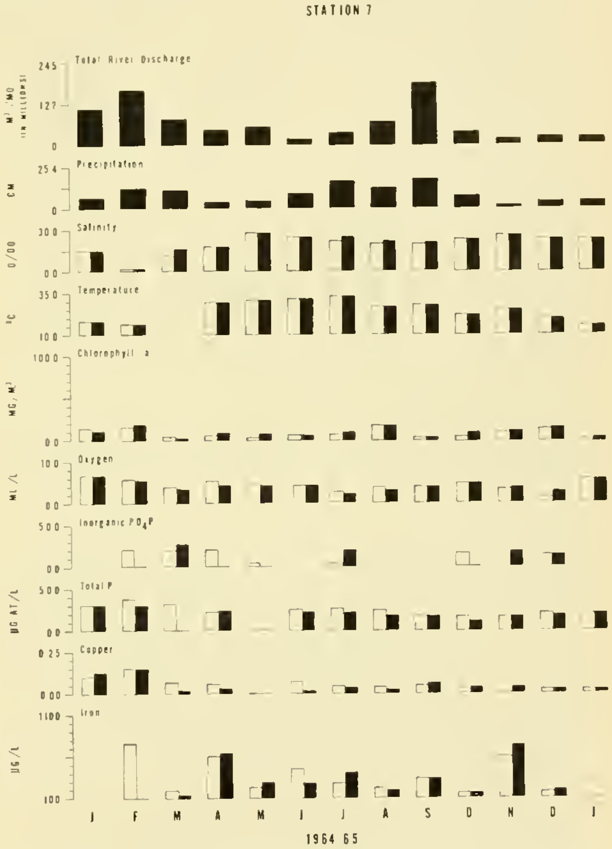

FIGURE 8.—River discharge, precipitation, and hydrological properties at station 7, Peace River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

DISSOLVED OXYGEN

Concentrations of dissolved oxygen at the river stations varied from 0.44 to 7.56 ml. per liter. Values were highest at most stations in winter and lowest in June and July (figs. 4–8). Oxygen values occasionally reached 100 to 142 percent saturation during every season. Most of the high values (stations 1, 2, 7, and 8) coincided with high concentrations of chlorophyll "a."

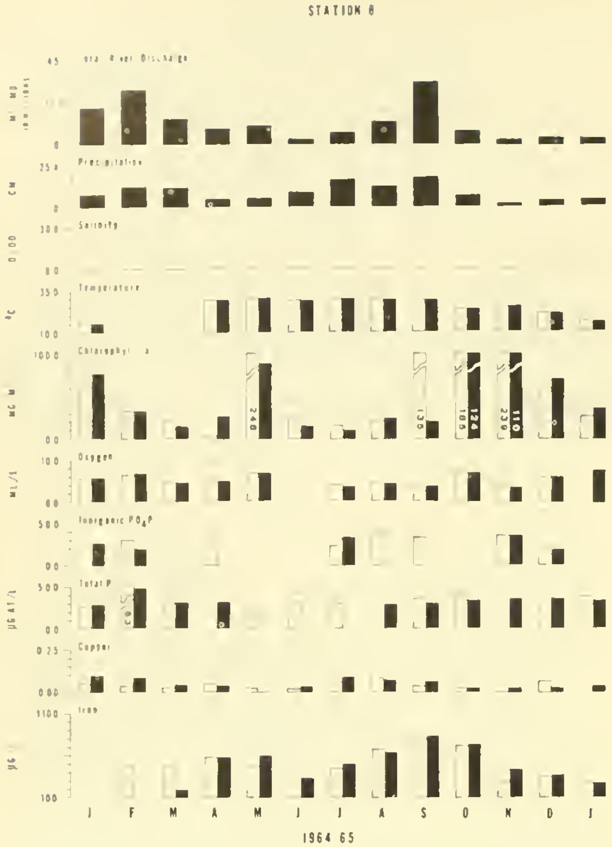

FIGURE 9.—River discharge, precipitation, and hydrological properties at station 8, Peace River, Fla., January 1964 to January 1965. (Open bars = surface; solid bars = bottom.)

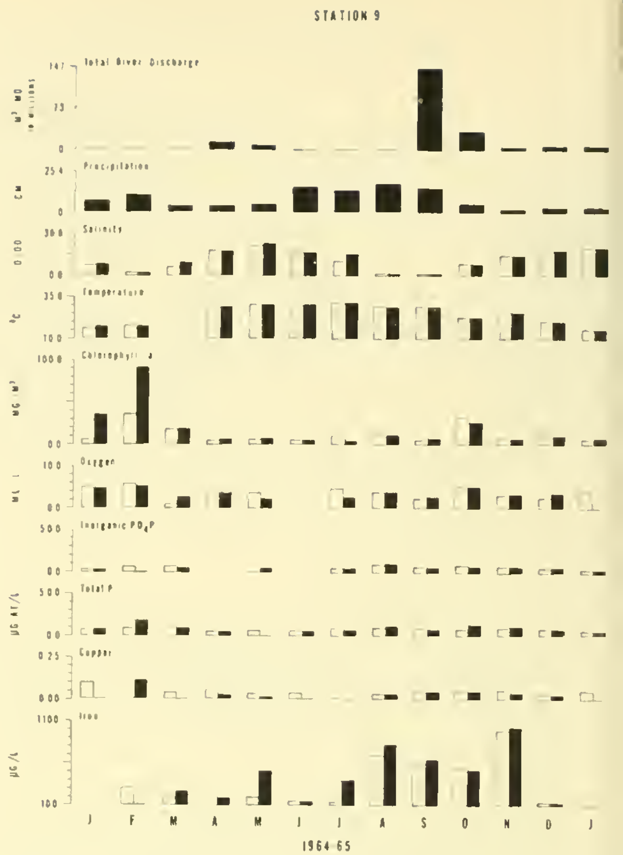

FIGURE 10.—River discharge, precipitation, and hydrological properties at station 9, Caloosahatchee River, Fla., January 1964 to January 1965. (Open bars = surface; solid bars = bottom.)

Even though anaerobic conditions were approached several times, no complete deoxygenation was detected. In 80 percent of the observations, oxygen saturation exceeded 50 percent. Values below 50 percent in one-fifth of the observations indicated that oxygen depletion occurred in the rivers. The occurrence of 75 percent of these values from April through September suggests that the depletion was seasonal.

Differences between surface and bottom values of oxygen were less than 1 ml. per liter in 84 percent of the observations. The similarity for most of the sets of observations reflects the capacity of the river system to maintain relatively high subsurface oxygen concentrations.

Irregularities in the vertical distribution of oxygen in periods of water stratification were associated with the presence of hydrogen sulfide near the bottom. Oxygen was almost exhausted near the bottom in the Hillsborough River (station 1) in April, June, August, and November (fig. 2).

TOTAL PHOSPHORUS

Concentrations of total phosphorus increased from downstream to upstream stations in the tributaries of Charlotte Harbor; Tampa Bay tributaries were sampled only at the mouths of rivers.

Quantities of total phosphorus were highest in the Peace River (station 8) and second highest in the Alafia River. Mean values at the surface and bottom in the Peace River (station 8) were 35.1 and 33.3 μg.at. per liter, and in the Alafia River (station 2) 27.5 μg.at. per liter, and 28.7 μg.at. per liter. At the remaining stations, the values for surface and bottom ranged from 4.2 to 23.5 μg.at. per liter. Values were lowest at the upstream station (10) in the Caloosahatchee River.

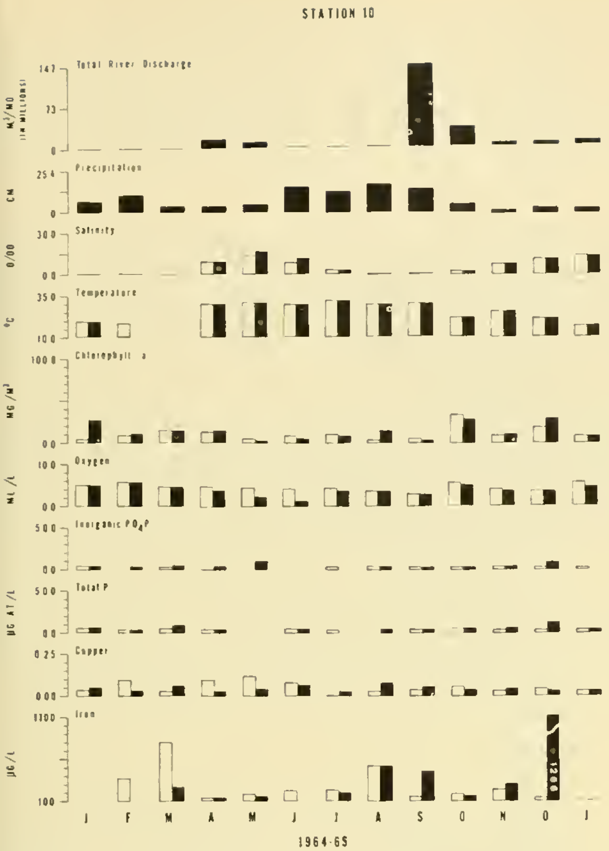

FIGURE 11.—River discharge, precipitation, and hydrological properties at station 10, Caloosahatchee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

Concentrations of total phosphorus in individual samples for all stations ranged from 3.1 µg.at. per liter in the Caloosahatchee River (station 10) to 62.9 µg.at. per liter in the Peace River (station 8).

The differences between surface and bottom values of total phosphorus varied from 0.0 to 15.4 µg.at. per liter. In the Hillsborough River (station 1) values were higher near the bottom than at the surface due to upstream intrusion of Hillsborough Bay water, in which phosphorus concentrations exceeded those in Hillsborough Bay (fig. 2, table 2). Salinity differences at surface and bottom substantiate the conclusion. This observation agrees with previous studies (Dragovich and May, 1962; Odum, 1953).

Vertical differences in salinity in the Alafia River (station 2) were not reflected in a pronounced vertical stratification of phosphorus (fig. 3). Concentrations of phosphorus in the river markedly exceed those in Hillsborough Bay (table 1). The discharge waters of the Alafia River are the chief source of phosphorus for Hillsborough Bay (Dragovich and May, 1962).

The Little Manatee River empties into the upper portion of Tampa Bay, and the Manatee River into the lower portion. Phosphorus concentrations in the upper and lower bays were similar to those in the Little Manatee and Manatee Rivers (table 1). Thus, the vertical stratification of phosphorus in these two rivers was usually moderate (figs. 4 and 5).

Phosphorus values generally were higher at the surface at stations 7 and 8. Differences between surface and bottom at stations 5 and 6 were slight. Values were higher at the bottom occasionally at both stations in the Caloosahatchee River. This situation may arise from the bottom sediment which enters the lower portion of the water column during periods of turbulence.

Monthly variations in total phosphorus showed no trend. Mean concentrations of total phosphorus at each river were multiplied by flow to estimate changes in the total monthly quantity of phosphorus. Combined calculations for all rivers showed maximum quantities in February, March, August, and September—the months with maximum runoff; values were low during the minimum runoff in June and November (table 4). It appears, therefore, that the quantity of phosphorus added to the bays and the adjacent sea depends more on volume of river flow than on concentrations of phosphorus in the streams. An exception was the Alafia River—the total quantity of phosphorus was much higher than in the Hillsborough River despite greater flow rate in the latter.

Geological formations influence the phosphorus content of the river water (fig. 12). The high phosphorus values are directly attributable to drainage areas that are highest in $CaPO_4$. Quantities were highest in the Peace and Alafia Rivers which flow primarily through Hawthorne phosphatic formations. Relatively high phosphorus concentrations in the Manatee, Myakka, and Peace Rivers may be explained by the fact that they flow through phosphorus-bearing formations (Bone Valley and Hawthorne). Higher values at the Hillsborough River station result from mixing of relatively phosphorus-rich bay water with river water. Concentrations were lowest in the Caloosahatchee River, only part of which drains

TABLE 4.—*Quantities of iron, total phosphorus, and copper discharged by Florida west coast tributaries*

[Metric tons]

River	1964												1965	Total
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	
	Iron													
Hillsborough		33.6	15.6	12.6	1.4	0.7	15.3	56.4	100.0	4.5	1.4	1.6	1.5	244.6
Alafia		49.9	6.7	3.2	6.3	1.9	4.3	10.6	19.4	7.4	2.0	2.1	6.8	120.6
Little Manatee		10.8	2.0	0.8	0.6	.1	1.3	2.6	3.6	0.6	0.2	1.6	0.2	24.4
Manatee		7.4	1.3	.7	.6	.2	0.4	2.9	1.3	.5	.2	0.1	.1	15.7
Myakka		8.9	6.6	5.6	.6	.1	1.0	10.3	18.8	1.7	.1	.2	.3	54.2
Peace		96.2	18.0	27.6	20.9	4.0	14.1	28.1	102.1	16.8	8.1	5.8	3.1	344.8
Caloosahatchee		0.2	0.6	1.6	2.3	.1	.2	0.5	64.6	11.3	2.5	3.1	.5	87.5
Total		207.0	50.8	52.1	32.7	7.1	36.6	111.4	309.8	42.8	14.5	14.5	12.5	891.8
	Total phosphorus													
Hillsborough		49.2	15.0	29.7	14.4	2.6	16.2	35.6	55.1	22.7	6.6	7.3	10.2	264.6
Alafia		61.3	26.0	9.0	26.1	9.0	18.9	56.2	30.6	18.2	8.2	12.4	16.2	292.1
Little Manatee		12.6	7.7	3.0	3.6	0.8	5.0	5.0	8.7	3.1	1.0	2.8	1.6	54.9
Manatee		6.0	3.0	1.1	0.8	.3		5.3	3.7	1.3	0.5	0.6	0.5	23.1
Myakka	6.8	6.1	3.6	2.6	.2	.1	0.5	6.8	10.9	1.1	.1	.1	.2	39.1
Peace	90.8	216.7	72.8	38.5	36.2	12.3	27.8	48.4	137.6	30.1	11.2	18.3	15.6	756.3
Caloosahatchee	0.1	0.2	0.4	1.8	1.6	.1	.1	0.2	27.9	8.2	.9	1.6	1.0	44.1
Total	97.7	352.1	128.5	85.7	82.9	25.2	68.5	157.5	274.5	84.7	28.5	43.1	45.3	1474.2
	Copper [1]													
Myakka	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1	<0.1	<0.1	0.8
Peace	.6	1.0	.2	.1	<.1	<.1	.1	.2	.6	<.1	<.1	<.1	<.1	3.1
Caloosahatchee	<.1	<.1	<.1	<.1	<.1	<.1	<.1	<.1	.4	<.1	<.1	<.1	<.1	.6
Total	.8	1.2	.2	.2	.1	.03	.2	.4	1.2	.2	.02	.05	.04	4.5

[1] All values of <0.1 in computation toward the total were not used; instead, actual values were used.

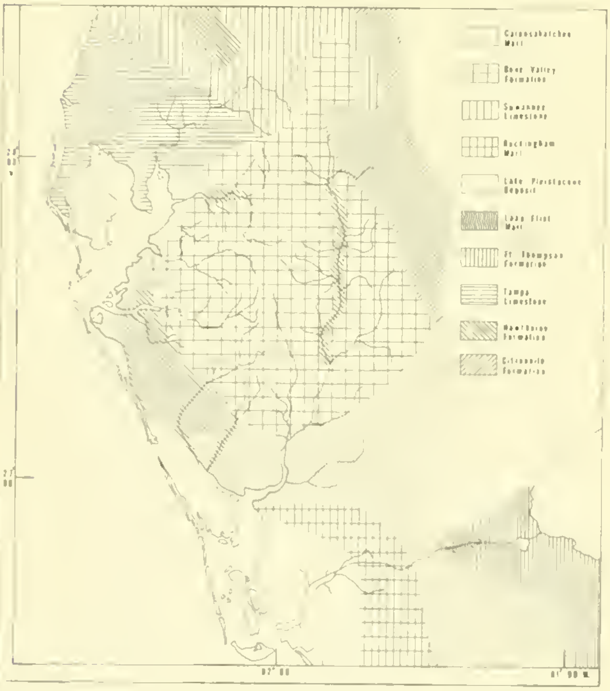

FIGURE 12.—Surface phosphate-bearing formations of the west coast of Florida (after Cooke, 1945). See table 5 for explanation of legend.

TABLE 5.—*Explanation of the legend for figure 12*

Geological formation	Composition
Caloosahatchee marl	Predominantly sand and shell marl.
Bone Valley formation	Phosphatic, sandy clay and gravel. Composition: 55-79% bone phosphate.
Suwannee limestone	Hard and resonant. Composition: 91-98% $CaCO_3$; chief impurity, silica.
Buckingham marl	Impermeable calcareous clay containing small grains of phosphatic material.
Lake Pleistocene deposits	Marine and estuarine deposits less than 30.5 meters above sea level.
Lake Flint marl	Calcareous fresh-water marl.
Ft. Thompson formation	Marine shell marl and fresh-water limestone.
Tampa limestone	Fairly hard and dense. Contains a large portion of very fine sand and phosphate. Composition: 74% calcium carbonate; <24% silica; trace magnesium carbonate.
Hawthorne formation	Sandy, phosphatic limestone, and green phosphatic clays.
Citronelle formation	Sand, gravel, and clay. The clay is kaolin when mixed with sand or gravel and is commonly iron stained.

through Buckingham marl formation (mainly impermeable calcareous clay containing only small grains of phosphatic material).

INORGANIC PHOSPHATE-PHOSPHORUS

The monthly changes and areal distribution of inorganic phosphate-phosphorus in all rivers were similar to those of total phosphorus (figs. 2-11). In 85 percent of the observations, inorganic phosphate-phosphorus exceeded organic and was responsible for the greater portion of total phosphorus. The quantities of phosphate-phosphorus always exceeded the minimum necessary for the growth of phytoplankters in vitro (Ketchum, 1939).

IRON

The study of the distribution of iron in Florida's west coast tributaries was undertaken for the first time in connection with the Florida red-tide studies. Thus, a few introductory remarks in regard to the importance of iron in the growth of phytoplankton seem to be appropriate. Iron occurs in many different physical and chemical forms in sea water (Ryther and Kramer, 1961). It may be present in generally unstable organic compounds that are slowly hydrolyzed in sea water (Harvey, 1937). The quantity of iron in true solution is extremely small because of the insolubility of ferric hydroxide.

The importance of iron in the physiology of phytoplankton has been stressed repeatedly (Harvey, 1957; Sverdrup, Johnson, and Fleming, 1942). Algae are able to use particulate iron as their major source of this element through ingestion by the protoplasm of particles of ferric hydroxide (Goldberg, 1952). Gran (1933) and Menzel and Ryther (1961) demonstrated the physiological dependence of phytoplankton on iron. Ryther and Kramer (1961) studied the relative iron requirements of some coastal and offshore planktonic algae. The consistency of their results demonstrates the importance of iron in determining the distribution of phytoplankton in the sea. Iron is beneficial in the culture of *Gymnodinium breve* (W. Wilson, personal communication). Even though the physiological importance of iron is known, no reliable techniques exist for determining the form in which it is available to phytoplankton (Harvey, 1937).

The concentration of iron in the sea is very small—from 0 to 10 μg. per liter (Ryther and Kramer, 1961). Quantities of this metal are much higher in drainage waters than in adjacent seas (Harvey, 1937).

The individual concentrations of iron in our study varied from 24.2 μg. per liter (at the surface in May at station 1, Hillsborough River) to 1540.4 μg. per liter (at the bottom in December at station 5, Peace River). The mean values for the entire period varied from 187.5 μg. per liter (at the surface of Little Manatee River) to 683.0 μg. per liter (at the bottom of Myakka River, station 6). Individual values were highest at the fresh-water stations in the Myakka and Peace Rivers and lowest in the Hillsborough River (figs. 2, 7, and 9). In 83 percent of all observations, iron values were from 50 to 599.0 μg. per liter; in 63 percent the concentrations were higher near the bottom than near the surface. The monthly changes in iron were very irregular at all stations (figs. 2–11) throughout the observation period.

Concentrations of iron in the rivers were several times higher than those in the adjacent sea and declined progressively in the seaward direction (table 1). River waters contribute iron to bay waters, but this influence is negligible offshore.

The highest concentrations of iron in the major rivers were in the area of limestone formation where the surface rock beneath the thin veneer of Pleistocene sands was either Miocene or Oligocene limestone. Iron values were intermediate in the major river (Myakka), which flows through Miocene phosphatic clays, and the difference was considerable between upriver values (station 5, fig. 6) and downriver values (station 6, fig. 7). This change can be directly attributed to the change from Pleistocene to Miocene deposits downstream. The lowest values were in the Alafia and Peace Rivers which flow through Pleistocene shelly sands of the Buckingham marl. The limestone areas are highly soluble to carbonated rain waters and carry the iron into solution with the $CaCO_3$. As long as iron is in the Fe^{+2} state, it moves readily; but when it is oxidized, it is precipitated as insoluble $Fe(OH)_3$. An occasional association between the increased rainfall and river discharge and higher iron concentrations was probably due to the oxidation of the iron in the limestone soils, and subsequent fixation. In times of high rainfall, iron moves into the rivers before oxidation can take place.

The total quantity of iron contributed to Gulf of Mexico waters by the rivers was estimated by multiplying average concentrations by flow. Even though monthly changes of iron concentrations at individual stations lacked a trend, combined data for all rivers showed that the contribution of iron by the rivers to the Gulf was greatest during maximum discharge (table 4).

COPPER

Concentrations of total dissolved copper at all stations varied from 0.00 to 0.23 µg.at. per liter. The levels were highest at fresh-water station 6 (Myakka River) and lowest at station 9 (Caloosahatchee River). In 82.5 percent of the observations, copper values were below 0.09 µg.at. per liter; 76 percent of the values that exceeded 0.09 µg.at. per liter were in the Myakka River. Although the highest values of copper came in January (0.08 µg.at. per liter), February (0.07 µg.at. per liter), and September (0.08 µg.at. per liter), at periods of high river discharge, the contribution of copper to the sea by the rivers was determined to a large extent by volume of river water, not by actual concentration.The largest total quantity of copper was contributed by the Peace River, and the lowest by the Caloosahatchee River (table 4).

Concentrations of copper were greater than those in Tampa Bay and adjacent waters of the Gulf of Mexico. The mean values for the Myakka River at station 6 exceeded those from Tampa Bay tributaries; values in the Peace and Caloosahatchee Rivers and at station 5 of the Myakka River were similar to the mean values for the Hillsborough, Alafia, and Manatee Rivers. Mean concentrations of copper were higher than those from San Juan Channel, Wash. (Chow and Thompson, 1952), but the mean concentrations at stations 5, 7, 8, and 9 are comparable with those reported by Chow and Thompson (1952) for the lower Mississippi River (table 6).

In general, changes in copper follow those of iron. This agreement results from the chemical scavenging of the colloidal $Fe(OH)_3$ for copper, which is absorbed to the surface of the particles.

Copper plays an important part in biological processes of higher aquatic organisms (Vinogradov, 1953; Galtsoff, 1964; Dragovich and May, 1962); it is adsorbed by phytoplankton (Atkins, 1953) and is selectively toxic to barnacles, algae, and mollusks. The dose of copper lethal to *Gymnodinium breve* under laboratory conditions is about 0.5 µg.at. per liter (W. Wilson, personal communication). None of the values observed in this study approached that level.

TABLE 6.—*Concentrations of total dissolved copper in Florida west coast rivers, Tampa Bay, and the adjaecnt Gulf of Mexico waters and in the Mississippi River and the San Juan Channel, Wash.*

Locality	Concentrations of copper			Reference
	Minimum	Maximum	Mean	
	µg.at./l.	*µg.at./l.*	*µg.at./l.*	
Hillsborough River:				Dragovich and May, 1962.
Station 29:				
Surface	0.02	0.07	0.04	
Bottom	.02	.09	.04	
Station 30:				
Surface	.02	.09	.05	
Bottom	.02	.08	.04	
Alafia River:				Do.
Station 31:				
Surface	.02	.16	.06	
Bottom	.03	.22	.06	
Station 32:				
Surface	.02	.08	.05	
Bottom	.01	.08	.04	
Little Manatee River:				Do.
Station 33:				
Surface	.03	.13	.07	
Bottom	.02	.12	.06	
Station 34:				
Surface	.02	.12	.08	
Bottom	.02	.13	.08	
Manateo River:				Do.
Station 35:				
Surface	.02	.11	.06	
Bottom	.02	.15	.06	
Station 36:				
Surface	.00	.16	.05	
Bottom	.01	.13	.04	
Myakka River:				Present study.
Station 5:				
Surface	.02	.12	.04	
Bottom	.02	.11	.05	
Station 6:				
Surface	.03	.17	.10	
Bottom	.02	.23	.10	
Peace River:				Do.
Station 7:				
Surface	.00	.16	.05	
Bottom	.00	.15	.04	
Station 8:				
Surface	.02	.08	.04	
Bottom	.01	.09	.04	
Caloosahatchee River:				Do.
Station 9:				
Surface	.00	.09	.03	
Bottom	.00	.11	.02	
Station 10:				
Surface	.00	.11	.04	
Bottom	.02	.11	.03	
Tampa Bay, Fla	.00	.09	.03	Dragovich, Finucane, and May, 1961.
Gulf of Mexico adjacent to Tampa Bay.	.00	.10	.03	Do.
Mississippi River	------	------	.04	Chow and Thompson, 1952.
San Juan Channel, Wash.	.012	.06	.023	Do.

RELATION OF THE INPUT OF FLORIDA WEST COAST TRIBUTARIES TO THE ABUNDANCE OF *GYMNODINIUM BREVE*

Water samples for analysis of *G. breve* were collected each month from 22 stations in Tampa Bay, Charlotte Harbor, and the adjacent offshore waters (Dragovich and Kelly, 1966). *G. breve* was absent in samples from Tampa Bay and present only twice in samples from Charlotte Harbor. In Gulf waters adjacent to Tampa Bay, Charlotte Harbor, and Pine Island Sound, *G. breve* was collected every month. Regression analysis was used to explore the relation between the mean monthly concentrations of *G. breve* and the weighted average input by the tributaries of Tampa Bay and Charlotte Harbor-Pine Island Sound. Weighted monthly inputs of iron, copper, phosphorus, and chlorophyll "a" for the tributaries were calculated by the formula:

$\overline{X}_{\%} = \overline{X}_{I} (I_{\%}) + \overline{X}_{II} (II_{\%}) + \overline{X}_{III} (III_{\%})$ . . . . etc.
where $\overline{X}$ is the average value of the variable, I, II, . . . at the station or river, and $I_{\%}$, $II_{\%}$, . . ., the percentage of the total monthly river discharge for a particular river.

Regression analysis was chosen because its requirements are not as strict as those for correlation, in which a normally distributed population is prerequisite. Two relationships were tested—polynomial and linear multivariate regression.

In the polynomial regression, each variable (total phosphorus, copper, iron, and chlorophyll "a") was taken as the independent variable, and *G. breve* as the dependent one. The linear, quadratic, and cubic regression relationships were calculated, and each tested for significance by analysis of variance. Relationships were insignificant at the 95-percent level. At the 80-percent level, the linear regression relationship between *G. breve* and iron was significant off both Tampa Bay and Charlotte Harbor. One reason for the weakness of this relationship may be that the independent variables were not measured at the places where *G. breve* was collected.

SUMMARY

A hydrological survey of Hillsborough, Alafia, Little Manatee, Manatee, Myakka, Peace, and Caloosahatchee Rivers, west Florida, was made from January 1963 to February 1964. Monthly changes in temperature, salinity, chlorophyll "a," dissolved oxygen, inorganic phosphate-phosphorus, total phosphorus, copper, and iron were determined. Data on precipitation and river discharges and general geomorphological features of the area are also given.

The water temperature data for all rivers varied from 12.8° C. (January 1965) to 32.4° C. (June and July 1964). Temperatures were low during December, January, and February and variably high from April through September. The vertical differences of temperature were insignificant.

Oligohaline (0.5 p.p.t. to 5 p.p.t.), mesohaline (5 p.p.t. to 18 p.p.t.), and polyhaline (18 p.p.t. to 30 p.p.t.) salinities were encountered at all but two fresh-water stations. Salinity was reduced in months of high rainfall and high river discharge.

The levels of chlorophyll "a" varied from 1.3 to 245.5 mg. per cubic meter and did not show the expected seasonal cycle of spring and autumn maximums and summer and winter minimums. The highest concentrations were in the Peace River at the fresh-water station.

No serious depletion of dissolved oxygen was indicated. In 80 percent of the observations, oxygen saturation exceeded 50 percent. Maximum values came in winter and minimums in summer. Some supersaturation was detected in every season.

Concentrations of inorganic phosphate-phosphorus and total phosphorus were high in all rivers; levels were exceptionally high in the Peace and Alafia Rivers which flow directly through an area rich in phosphatic formations. Inorganic phosphate-phosphorus was responsible for most of the phosphorus.

Copper values varied from 0.00 to 0.23 μg.at. per liter and were higher than those in the adjacent Gulf of Mexico. They were markedly below the lethal dose for *Gymnodinium breve.*

The concentrations of iron were several times higher in the rivers than in the adjacent Gulf of Mexico waters. Values were highest at the fresh-water stations in the Myakka and Peace Rivers and lowest in the Hillsborough River. Temporal changes in iron lacked a distinct trend.

Variation in rate of flow has a marked effect on the total quantities of the materials in the rivers.

The polynomial regression between total phosphorus, copper, iron, chlorophyll "a" as the independent variable and abundance of *G. breve* as the dependent variable revealed no relationships significant at the 95-percent level; iron and *G. breve* were directly related at the 80-percent level of significance in coastal waters off Tampa Bay and Charlotte Harbor.

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INTRAGRAVEL FLOW AND INTERCHANGE OF WATER IN A STREAMBED

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ABSTRACT

The chemical quality of intragravel water in streams—the environment of salmon eggs, embryos, and alevins—is influenced by the rate of interchange of stream water and intragravel water. Factors controlling the direction and magnitude of flow or interchange of this water were identified in this study. Equations describing motion of waterflow within the streambed under specified boundary conditions are developed, and tests of the mathematical model with an electrolytic bath analog model are described.

The direction of waterflow within a streambed and the interchange of water between the bed and the stream depend primarily on the permeability, depth, and longitudinal profile of the porous streambed. Water upwells where permeability or depth of gravel decreases in the direction of streamflow and where the longitudinal bed profile is concave. Water downwells where permeability or depth of gravel increases in the direction of streamflow or where the longitudinal bed profile is convex.

Embryos and alevins of Pacific salmon (genus *Oncorhynchus*) live in gravel beds of streams for as long as 9 months before the fry emerge. The young salmon may be subjected to a poor chemical environment because of the low waterflow in the spawning bed. In laboratory experiments, oxygen privation and reduced waterflow, alone or together, impaired growth and development of salmonid embryos and caused mortality (Silver, Warren, and Doudoroff, 1963; Shumway, Warren, and Doudoroff, 1964). In natural streams, mortality of salmon spawn was high when the supply of dissolved oxygen in intragravel water (water occupying interstices within the streambed) became low (Phillips and Campbell, 1962; McNeil, 1966). Dissolved waste metabolites are known to be harmful to fishes: high levels of free carbon dioxide reduce the blood's affinity for oxygen, and un-ionized ammonium hydroxide is highly toxic to alevins (McNeil, Wells, and Brickell, 1964). The concentration of waste metabolites in the water surrounding organisms generating the wastes varies inversely with the rate of flow of intragravel water. It is, therefore, necessary that the velocity of intragravel flow be adequate to assure low concentrations of waste metabolite.

Because the primary source of oxygen and the water flowing through the gravel in many salmon spawning beds is stream water, the processes that regulate interchange between intragravel water and stream water are important in the ecology of salmon spawning beds. The purpose of my study is to identify some of the variables that control this interchange. In an earlier paper (Vaux, 1962), I related the direction of interchange to streambed shape from a mathematical model and presented field data which demonstrated that the relation was correct.

This paper treats the theory of flow of intragravel water in detail and gives the results of my laboratory experiments in which intragravel flow and interchange were simulated with an analog model. The means by which interchange can be controlled to improve water quality within salmon spawning beds are discussed.

I started my study of the movement of water within streambeds in 1958 while employed at the Fisheries Research Institute of the College of Fisheries, University of Washington. The experimental work and some of the mathematical formulation were completed in 1960–61 as part of a thesis, which was submitted to the Department

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of Chemical Engineering, University of Minnesota (Vaux, 1961).

All symbols are defined the first time they appear and are listed with definitions and units in the "Notation" section near the end of this paper.

THEORY OF INTRAGRAVEL WATERFLOW

Charles Slichter (1899) first applied the mathematics of partial differential equations to the motion of groundwater (waterflow in saturated soil). His formulation of the equations describing groundwater flow provided a foundation for subsequent analyses of similar problems of intragravel waterflow.

In developing the theory of intragravel waterflow, I treat the case where the rate equation for flow in porous media is linear, i.e., conditions under which Darcy's law applies. Ergun (1952) showed that for a given particle size and bed porosity, the ratio of pressure gradient to water velocity in a porous bed is given by $(\Delta P/L)/v \propto (c_1+c_2N_{Re})$ where c_1 and c_2 are known constants, and N_{Re} is the Reynolds number based on particle diameter. The constants c_1 and c_2 respectively account for pressure loss from the effects of viscous and kinetic energy. The expression $(\Delta P/L)/v \propto c_1$, called Darcy's law, is considered applicable for Reynolds numbers less than unity (Rumer, 1965). Although flow may be laminar in situations where the Reynolds numbers are higher than unity, the effects of convective acceleration in such situations invalidate Darcy's law (Silberman, 1965).

Analysis of data on gravel size, permeability, and hydraulic gradient from the Carmen-Smith spawning channel,[1] and Jones Creek, Alaska, spawning channels, McNary, Priest Rapids, and Robertson Creek,[2] and my data from Sashin Creek, Alaska, indicates that intragravel flow is of the linear laminar type and, therefore, described by Darcy's law. I assume that these cases describe the usual conditions in salmon spawning beds and that Darcy's law is generally applicable in the description of intragravel flow.

For situations in which the Reynolds numbers are less than unity, the velocity of laminar seepage flow within a porous medium, v, is related to the pressure gradient, $\Delta P/L$ by

$$v=-k\frac{g_c}{\mu}\frac{\Delta P}{L} \tag{1}$$

This relation is termed Darcy's law, but rather than a law, it is actually an equation which defines k, the "specific permeability," or just "permeability." In equation (1), μ is the liquid viscosity, and g_c is the constant of Newton's second law, introduced to make the equation dimensionally correct (g_c equals 1 g.-cm./dyne-sec.^{2} in centimeter-gram-second units).

The value of ΔP can be calculated by the relation $\Delta P=\rho\frac{g}{g_c}\Delta h$, where ρ is liquid density, Δh is head loss over the distance L, and g is acceleration due to gravity. Figure 1 illustrates the variables v, k, Δh, and L. The head loss, Δh, is shown in figure 1 by the elevations to which water rises in the piezometer tubes at opposite ends of the column of porous material.

We may extend Darcy's law to account for flow due to gravity, in addition to pressure, and write expressions for velocity in each of the three directions of a cartesian coordinate system. Ratios for $\Delta P/L$ can be replaced with the corresponding derivatives:

$$v_x=-k\frac{g_c}{\mu}\frac{\partial P}{\partial x} \tag{2a}$$

$$v_y=-k\frac{g_c}{\mu}\left(\frac{\partial P}{\partial y}+\frac{g\rho}{g_c}\right) \tag{2b}$$

$$v_z=-k\frac{g_c}{\mu}\frac{\partial P}{\partial z} \tag{2c}$$

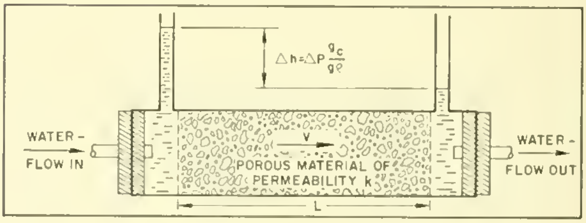
$\Delta h=\Delta P\frac{g_c}{g\rho}$
WATER - FLOW IN
V
POROUS MATERIAL OF PERMEABILITY k
WATER - FLOW OUT
L

FIGURE 1.—Rectilinear waterflow through a sample of porous material showing a head loss $\Delta h=\Delta P\frac{g_c}{g\rho}$ over a distance L.

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[1] Hagey, Dale W., and Robert T. Gunsolus, Progress report on the operation and evaluation of the Carmen-Smith spawning channel, 1960–64. Oregon Fish Commission, Feb. 1965, 12 pp.

[2] Data supplied by the Columbia Fisheries Program Office, Bureau of Commercial Fisheries, Portland, Oreg.

The coordinate system has been oriented so that the y direction is vertical and parallel to the direction of gravity. In equations (2) we assume that permeability is the same in every direction.

Equations (2) imply the single vector equation

$$\mathbf{i}v_x+\mathbf{j}v_y+\mathbf{k}v_z=-k\,\frac{g_c}{\mu}\left[\mathbf{i}\,\frac{\partial}{\partial x}\,(P)+\mathbf{j}\,\frac{\partial}{\partial y}\left(P+\frac{\rho g y}{g_c}\right)+\mathbf{k}\,\frac{\partial}{\partial z}\,(P)\right]$$

or

$$v=-k\,\frac{g_c}{\mu}\,\nabla\left[P+\frac{\rho g y}{g_c}\right] \tag{3}$$

where ∇ is the gradient operator defined by $\nabla\equiv\mathbf{i}\,\frac{\partial}{\partial x}+\mathbf{j}\,\frac{\partial}{\partial y}+\mathbf{k}\,\frac{\partial}{\partial z}$ and $\mathbf{i}$, $\mathbf{j}$, and $\mathbf{k}$ are unit vectors respectively in the three mutually perpendicular directions of the distance variables x, y, and z.

For later application of Darcy's law it is convenient to define the expression $\phi\equiv\frac{g_c P}{g\rho}+y$ and rewrite equation (3) as

$$v=-k\,\frac{\rho g}{\mu}\,\nabla\phi \tag{4}$$

Note that ϕ, the potential for intragravel flow, represents the total energy of intragravel water and is the sum of pressure energy and elevation energy. Kinetic energy is assumed to be negligible.

The continuity equation or equation of conservation of mass for an incompressible fluid is

$$\nabla\cdot\mathbf{v}=0 \tag{5}$$

The substitution of Darcy's law, equation (4), into equation (5) gives

$$k\nabla^2\phi+(\nabla k)\cdot\nabla\phi=0 \tag{6}$$

If the permeability, k, is homogeneous or uniform (i.e., independent of position) equation (6) reduces to Laplace's equation,

$$\nabla^2\phi=\frac{\partial^2\phi}{\partial x^2}+\frac{\partial^2\phi}{\partial y^2}+\frac{\partial^2\phi}{\partial z^2}=0 \tag{7}$$

Meaningful solutions of equation (6) or (7) cannot be found until the boundary conditions (i.e., the values of ϕ or derivatives of ϕ along the boundaries of the porous bed) are specified.

I have thus far discussed any laminar flow described by Darcy's law. Components of waterflow within a streambed are shown in figure 2. The porous streambed, A, is considered to be a stable bed consisting of particles and having a uniform permeability, k. The ambient stream, B, is continuous and uniform. The porous streambed is bounded below by an impermeable stratum, C. Any flow, D, within the porous bed is termed intragravel flow and is characterized by a velocity vector, $\mathbf{v}$. Any flow across the upper boundary of the bed is termed interchange. An upward interchange from the bed to the stream is upwelling, F; a downward interchange is downwelling, E.

The above conditions of uniform permeability and an impermeable stratum, for which equation (7) applies, characterize most manmade spawning channels. The permeability of natural streambeds usually decreases with depth, and flow is described by equation (6). Where permeability varies with depth, one may measure permeability at several depths and assign an appropriate permeability function, $k(y)$.

Equation (6) or equation (7) for uniform permeability characterizes all laminar flow through porous materials; the boundary conditions distinguish particular seepage situations. Our consideration of intragravel flow is limited to a two-dimensional system for which four boundary conditions must be specified about a bed of finite dimensions. An infinitely long bed requires specification of two boundary conditions. Because there is no flow across the lower boundary of the porous bed, the component of waterflow normal to the boundary at the boundary is 0 and

$$\left.\frac{\partial\phi}{\partial n}\right|_{\text{boundary},\ y_2(x)}=0 \tag{8a}$$

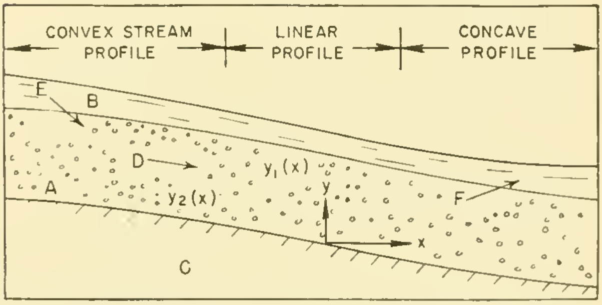

FIGURE 2.—Description of terms and properties relating to waterflow within a streambed. A, porous bed; B, ambient stream; C, impermeable stratum; D, intragravel flow; E, downwelling; F, upwelling; y_1, bed surface profile; y_2, impermeable stratum profile.

where n is the direction normal to the impermeable surface.

The velocity vector at any point within a streambed is influenced by streambed geometry and boundary conditions over the length of the stream. For investigation of intragravel flow in a finite reach of stream, between $x=0$ and $x=a$, we ignore upstream and downstream conditions. The boundary conditions $\phi(0,y)$ and $\phi(a,y)$ depend upon conditions over all the streambed. Since $\phi(x, y_1(x))$, hereafter denoted by $\phi(x)$, is unknown outside of $0 \leq x \leq a$, it is necessary to assign reasonable estimates of ϕ along the upstream and downstream boundaries of the isolated region. Accordingly, in isolating a region of streambed of depth b between $x=0$ and $x=a$, I specify the boundary conditions $\phi(0,y)$ and $\phi(a,y)$ to be constant and respectively equal to $\phi(0,b)$ and $\phi(a,b)$. The physical model is shown in figure 3(i)

$$\phi(0,y)=\phi(0,b) \tag{8b}$$

$$\phi(a,y)=\phi(a,b) \tag{8c}$$

Because of continuity of pressure across the stream-gravel interface, the potential at the upper bed boundary, $\phi[x, y_1(x)] \equiv \phi(x)$, must be equal to the potential at the bottom of the contiguous flowing stream. The problem of determining the potential along the upper boundary, $\phi(x)$, then becomes one of hydraulics.

The bottom pressure, $P(x,y_1)$, of a flowing stream is related to properties of the stream by

$$P(x,y_1)=\frac{\rho g}{g_c}d(x)+P_o+P_c(x,y_1) \tag{9}$$

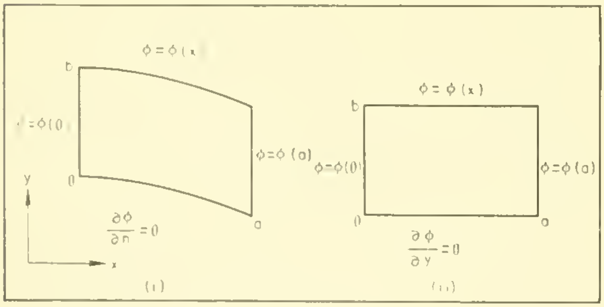
ϕ = ϕ (x
b
=ϕ(0
ϕ=ϕ (a)
y
0
$\frac{\partial\phi}{\partial n}=0$
a
x
(i)
ϕ = ϕ (x)
b
ϕ=ϕ(0)
ϕ=ϕ (a)
0
a
$\frac{\partial\phi}{\partial y}=0$
(ii)

FIGURE 3.—(i) Boundary value problem representing the physical model for flow through a streambed of porous material. The shape of the region is the actual shape of the porous bed in which the upper and lower boundary curves are the topographical profiles of the bed surface and impermeable layer. (ii) Part (i) mapped into a rectangle.

in which $d(x)$ is the stream depth, P_o is atmospheric pressure, and P_c is centrifugal pressure due to stream curvature. From a stream-continuity equation, $d(x)U(x)=\text{constant}$, and the Manning flow formula,[3] $U(x)d(x)^{-2/3}\ y'1(x)^{-1/2}\simeq\text{constant}$, where y' is the hydraulic gradient and U is the average stream velocity, I find that the stream depth varies with the 0.3 power of hydraulic gradient. Considering small changes in stream gradient so that changes in $P_c(x)$ and $d(x)$ are small, it follows that changes in the right-hand side of equation (9) are small compared with changes in $y'(x)$ and that $g_cP/g\rho\simeq\text{constant}$, from which we may approximate the potential of the upper bed boundary

$$\phi(x)=y_1(x)+\frac{g_cP(x,y_1)}{g\rho}\simeq y_1(x)+\text{constant} \tag{8d}$$

The applicability of equation (8d) is limited to reaches of nearly constant stream depth (see footnote 3). Because the average velocity of streamflow is several orders of magnitude greater than the velocity of intragravel flow, the influence of interchange on stream discharge is negligible.

Equation (6) or equation (7) for uniform permeability and the equations for the four boundary conditions (8a–8d) complete the boundary value problem. Figure 3(i) depicts the model that is considered for particular solutions. Solution of the boundary value problem is facilitated by assuming the bed to be of constant depth, b (so that $y_1=y_2+b$ (fig. 2)) and by mapping the irregularly bounded region into a rectangle, as in figure 3(ii). The error introduced is negligible because, over short distances (e.g., less than 10 m.), natural streambeds commonly have almost constant depth and are nearly horizontal. Boundary potentials are unchanged by formation of a rectangle.

Analytical solutions of the boundary value problem describing intragravel flow usually involve the use of infinite series, i.e., are of open form. Two simple closed-form solutions arise in the methods used here to solve the problem.

1. A potential $\phi(x)=\phi(0)-\phi(0)x/a+p\sin(\pi x/a)$ in which p is an arbitrary constant holds in a curved streambed surface profile for $0<x<a$. According to equation (8d) the profile has a

---

[3] This form of the Manning equation implies that the stream hydraulic radius is equal to $d(x)$, that bed roughness is constant in the direction of flow, and that the stream energy gradient is parallel to the streambed surface.

negative slope and is convex if $0<p\leq\phi(0)/\pi$, and concave if $0>p\geq-\phi(0)/\pi$ (See figure 2). The solution to the boundary value problem equation (8a-d) for this surface potential and a bed of uniform permeability is

$$\phi(x,y)=p\,\frac{\cosh(\pi y/a)}{\cosh(\pi b/a)}\sin(\pi x/a)+\phi(0)-\frac{\phi(0)x}{a} \tag{10}$$

If we define interchange as the vertical (y-directed) component of intragravel flow at the streambed surface (fig. 2) the exact magnitude of interchange is given by

$$\mathbf{v}_{y|y=b}=-k\,\frac{\rho g}{\mu}\,\frac{\partial\phi}{\partial y}\,\mathbf{j}_{\,|y=b} \tag{11}$$

For the example at hand the interchange velocity is

$$\mathbf{v}_{y|y=b}=-k\,\frac{\rho g}{\mu}\,\frac{\pi p}{a}\tanh\frac{\pi b}{a}\sin\frac{\pi x}{a}\,\mathbf{j} \tag{12}$$

This example shows that the direction of interchange depends on the shape of the streambed surface. A convex streambed profile for which p is positive induces a negative interchange velocity or downwelling; a concave profile for which p is negative causes upwelling.

2. Statement of the boundary value problem for an infinitely long streambed requires only equations (6), (8a), and (8d). We may solve the boundary value problem for the flow within an infinitely long streambed by the mathematics of complex variables (Weinberger, 1965, pp. 201–268). The transformation $\zeta=(\cosh Z-1)/\sinh Z$ conformally maps an infinitely long streambed of depth $b=\pi/2$ in the Z plane into a half disk in the ζ plane. The boundary potential $\phi(x)=-q\tanh x$ for $-\infty<x<\infty$ where q is a positive dimensionless, adjustable parameter is associated with the sigmoid-shaped streambed in figure 2. The solution of the boundary value problem is $\phi(x,y)=-q\sinh x/(\cosh x+\cos y)$. From equation (11) we find the interchange velocity to be

$$\mathbf{v}_{y|y=b}=kq\,\frac{\rho g}{\mu}\,\frac{\sinh x}{\cosh^2 x}\,\mathbf{j} \tag{13}$$

As in the previous example, downwelling takes place in a convex streambed profile $(-\infty<x<0)$ and upwelling in a concave profile $(0<x<\infty)$.

ANALOG MODEL INVESTIGATION OF INTRAGRAVEL FLOW

An electrolytic-bath analog model was used to solve the boundary value problem (equations 7 and 8a–8d) for several specified boundary conditions and a streambed of uniform permeability. This technique of solving the partial differential equations of intragravel flow rests upon the analogy between Darcy's and Ohm's laws and the respective steady-state conservation equations of mass and electrical charge. An electrolytic equivalent of a streambed section with intragravel flow can be prepared by constructing a shallow tray geometrically similar to the two-dimensional porous bed. The depth of the conducting liquid at any point in the tray is proportional to the permeability at the corresponding point in the porous bed. The conducting tray walls, usually metal strips, are set at voltages proportional to the analogous hydrodynamic flow potentials or values of ϕ (Zangar, 1953, p. 24).

EQUIPMENT AND PROCEDURE

The electrolytic-bath model constructed for this investigation was a 10- by 20-cm. plexiglass tray filled to a depth of 2.5 cm. with a 0.01 normal solution of aqueous sodium chloride (fig. 4). The end walls representing constant potential (constant ϕ) surfaces were brass strips; a nonconducting strip represented a water-impermeable surface. Rheostat-controlled voltages applied separately to each of 15 electrodes along the variable-potential wall ($y=b$) provided an approximation to the potential function, $\phi(x)$.

In all operations of the analog model, 10 volts of 60-cycle alternating current were impressed

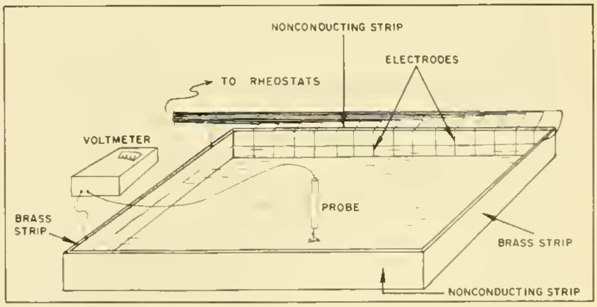

Figure 4.—Electrical circuits and physical layout for electrolytic-bath analog model used to investigate flow of intragravel water in a streambed.

between the brass strips; appropriate intermediate voltages were applied to the electrodes.

Solutions of the partial differential equation for different boundary conditions were obtained by tracing with a probe connected in series with a voltmeter and one tray wall along constant potential lines in the electrolyte. Results were recorded with a pantograph.

DIRECTION OF FLOW

Figures 5 through 9 represent longitudinal cross sections of a streambed: the top surface of the figure represents the upper surface of the streambed and the bottom, the impermeable stratum. The right and left ends of each figure represent arbitrary vertical planes bounding the reach of streambed considered. The lines of constant

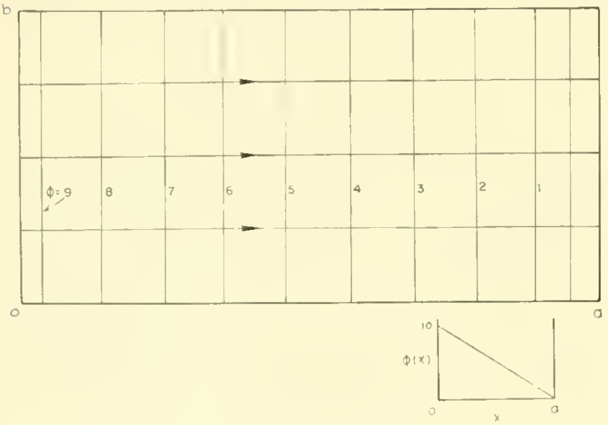
b
φ=9
8
7
6
5
4
3
2
1
0
a
10
φ(x)
0
x
a

FIGURE 5.—Flow net for straight-line-surface potential $b/a=\frac{1}{2}$.

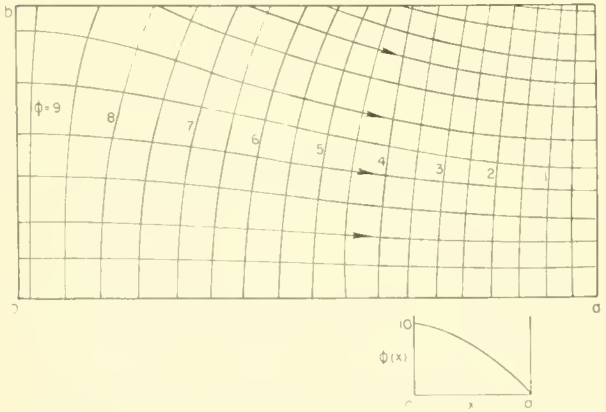
b
φ=9
8
7
6
5
4
3
2
1
a
10
φ(x)
x
a

FIGURE 6.—Flow net for convex parabolic surface potential.

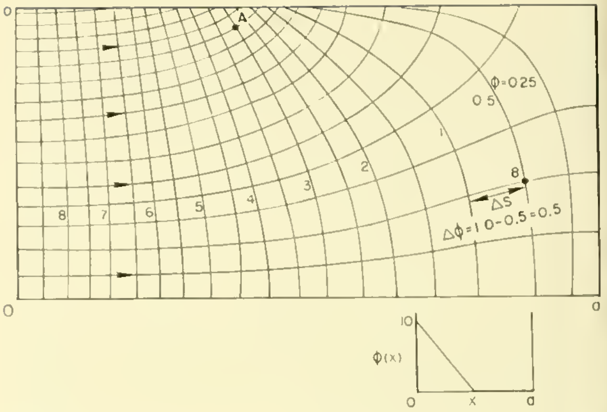
A
φ=0.25
0.5
1
2
3
4
5
6
7
8
B
Δs
Δφ=1.0-0.5=0.5
0
a
10
φ(x)
0
x
a

FIGURE 7.—Flow net for concave broken-line-surface potential, illustrating evaluation of Δs and $\Delta\phi$.

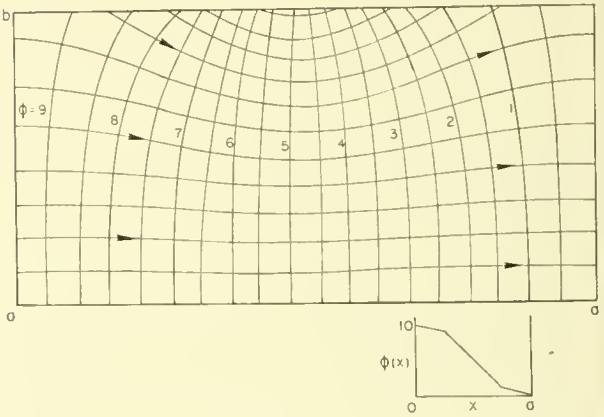
b
φ=9
8
7
6
5
4
3
2
1
0
a
10
φ(x)
0
x
a

FIGURE 8.—Flow net for sigmoid surface potential.

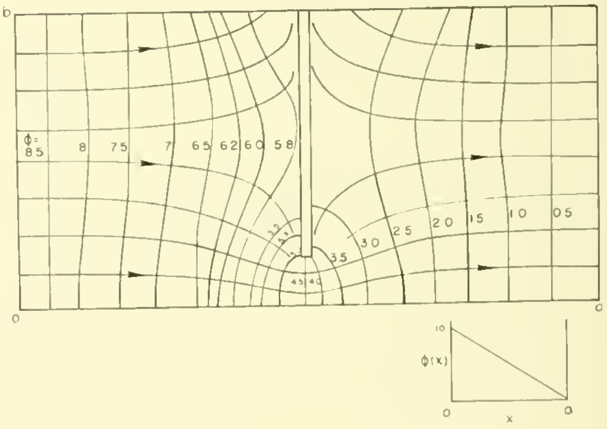
b
φ= 8.5
8
7.5
7
6.5
6.2
6.0
5.8
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
a
10
φ(x)
0
x
a

FIGURE 9.—Flow net for straight-line surface potential with impermeable intragravel barrier at $x=0.5a$, $b/a=\frac{1}{2}$.

potential, shown in the figures to be approximately vertical, were obtained from the analog model; the intragravel flow streamlines were later drawn normal to the constant potential lines to obtain a grid of "curvilinear squares" (Zangar, 1953, p. 17). Actually, the lines of constant potential shown are the analogs of the recorded lines of constant voltage, and the intragravel flow streamlines are the analogs of electrical current vectors. Figures 5, 6, 7, and 8 show the flow nets corresponding to certain of the boundary potential functions, $\phi(x)$, investigated. Figure 9 shows the effect of changed permeability on flow.

EFFECTS OF STREAMBED CHARACTERISTICS ON WATER INTERCHANGE

Accompanying each of the analog solutions shown in figures 5 through 9 is a small figure showing the function, $\phi(x)$, investigated. Since the flow potential along the open surface is approximately the elevation of the porous bed surface plus a constant, i.e., $\phi(x)=y_1(x)+\text{constant}$, each of the graphs is, in effect, a longitudinal profile of the streambed associated with the function. Figure 5 shows the pattern of intragravel flow within a streambed whose surface is straight. The profile of figure 6 may be viewed as a longitudinal convex stream section. Figure 7 illustrates the intragravel flow expected in the streambed beneath and beyond a rapids.

Figure 8 illustrates intragravel flow near a riffle between two low-gradient stream sections. This pattern of intragravel flow typifies the mechanism by which respiring salmon eggs and alevins are supplied with dissolved oxygen. Freshly oxygenated water downwells into the streambed, passes through the streambed's interior where oxygen is removed by salmon embryos or alevins, and upwells back into the stream.

The effect of placing a sheet piling in the gravel bed is shown by comparing the flow net of figure 5 with that of figure 9. Note that the streambed-surface potential, $\phi(x)$, in figure 9 is the same as that in figure 5 where, in the absence of a sheet piling, there is no interchange. The sheet piling directs intragravel flow to the surface upstream and induces downwelling downstream of the piling. The extent of interchange induced depends on the depth to which the piling is driven and the nearness of its bottom edge to an impermeable stratum.

Figures 5, 6, 7, and 8 show that the flow nets are characterized by variable directions of interchange: upwelling, downwelling, or interchange in both directions. Furthermore, the x-directed component of intragravel flow is always positive. From an analysis of many similar analog solutions and from observations in natural streams, I have found that downwelling occurs in longitudinally convex stream sections, as illustrated in figure 6. Similarly, upwelling takes place in longitudinally concave stream sections.[4]

Natural stream profiles usually contain alternate convex and concave reaches which cause alternate regions of upwelling and downwelling of stream water into and from the streambed. The penetration depth of this interchange flow depends on streambed geometry, e.g., the amount of curvature of the bed surface and depth of the streambed. In artificial spawning channels of uniform depth of streambed and uniform permeability, the bed surface is often groomed to an almost flat surface, and almost no potential exists for interchange. The movement of oxygen-rich water into the streambed must be by mechanisms other than normal water interchange, such as mechanical dispersion.

The flow nets of figures 5 through 9 show relative magnitude as well as direction of intragravel flow. Velocity of intragravel flow varies inversely with distance between lines of flow potential. When the lines are closely spaced, as at point A in figure 7, intragravel flow velocity is high. Widely spaced lines, as at point B in figure 7, show a low velocity of intragravel flow. Numerical values of velocity are calculated from equation (4), through use of a value of

$$|\nabla\phi|\simeq\frac{\Delta\phi}{\Delta s},$$

taken from the flow net as illustrated in figure 7 ($\Delta\phi$ is read as "the change in ϕ"). The symbol s is the distance variable along a streamline. The streamlines indicate the direction of intragravel flow.

---

[4] A. C. Cooper (1965), in a study of intragravel flow in salmon redds, showed results of intragravel backflow, $v_x<0$, and upwelling beneath a convex streambed surface. For this geometry the small radius of curvature of the streambed surface does not allow the approximation of equation (8d), and the boundary condition at the streambed surface, $\phi(x)$, must be obtained by a more rigorous approach. The geometry of Cooper's model studies suggests counter pressure gradients at the streambed surface and reaches of strongly variable streambed depth in the direction of flow. Such conditions would account for an upstream flow of intragravel water.

Errors in the technique included resistance heating of the electrolyte and polarization of the electrodes. The effect of polarization is shown where the potential gradient near the equipotential wall at $x=0$ is particularly steep.

The solutions of figures 5 through 9 for $b/a=1/2$ are not affine solutions; that is, they cannot be "stretched out" to describe exactly the intragravel flow in porous beds of different depth-length ratios. The flow nets shown, however, bear resemblance to and have the same general dependence on boundary-potential shape as rectangular beds of any depth-length ratio.

We have seen that for uniform permeability and constant bed depth, direction and magnitude of interchange depend upon configuration of the streambed surface. Direction and magnitude of interchange vary as well with longitudinal variations in depth and permeability of the streambed.

Consider the streambed section of figure 10. For this section the intragravel-flow streamlines will have a form somewhat like that shown in section C. Assume that all streamlines are parallel to the lower bed boundary, as in B of figure 10, and that water leaves or enters the streambed by a y-directed velocity (interchange) concentrated at the upper bed boundary, $y=b$ (see Lubyako, 1956, for discussion of this assumption). By a mass balance about the lamina of depth, b, width, w, and thickness, Δx, shown in A of figure 10,

$$\rho b w v_x|_x - \rho b w v_x|_{x+\Delta x} = v_y w \Delta x \rho. \qquad (14)$$

In the limit as Δx approaches zero, the interchange, $v_y|_{y=b}$, is given by

$$v_y \Big|_{y=b} = -\frac{d}{dx}(b v_x). \qquad (15)$$

Combining equation (15) with Darcy's law for the x-directed component of velocity

$$v_x = -k \frac{\rho g}{\mu} \frac{d\phi}{dx}, \qquad (16)$$

and equation (8d) yields

$$v_y \Big|_{y=b} = \frac{\rho g}{\mu} \frac{d}{dx} \left(bk \frac{dy^1}{dx} \right). \qquad (17)$$

Equation (17) agrees with the analytical and analog results for interchange direction. For constant bed depth, d, and permeability, k,

$$v_y \Big|_{y=b} = \frac{\rho g}{\mu} bk \frac{d^2 y_1}{dx^2}. \qquad (18)$$

For a longitudinally convex streambed surface, d^2y_1/dx^2 is negative, and equation (18) implies a downwelling. Conversely, equation (18) indicates upwelling with a concave streambed surface.

From equation (17) I have summarized in table 1 the dependence of interchange upon streambed permeability and geometry, both of which may be regulated to control the direction of interchange. Assuming that the permeability of a streambed may be increased by removing fine materials (Krumbein and Monk, 1942; McNeil and Ahnell, 1964) or that the effective gravel-bed depth (i.e., depth to which intragravel flow can occur) may be increased by removing fine particles from lower strata, it should be possible to create the interchange patterns shown in figures 11, 12, and 13. It should also be possible to control direction and amount of interchange in salmon spawning areas by varying the streambed-surface profile (fig. 14).

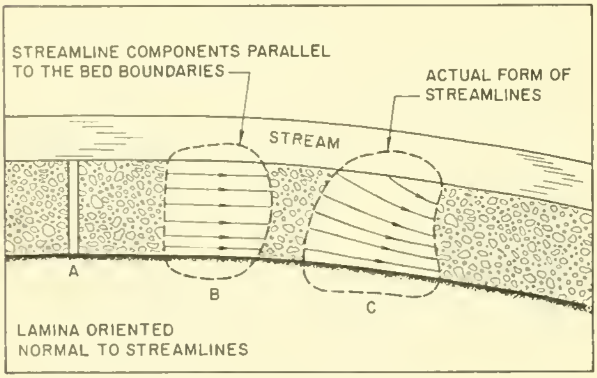
STREAMLINE COMPONENTS PARALLEL TO THE BED BOUNDARIES
ACTUAL FORM OF STREAMLINES
STREAM
A
B
C
LAMINA ORIENTED NORMAL TO STREAMLINES

FIGURE 10.—Idealized concept of intragravel flow in a streambed.

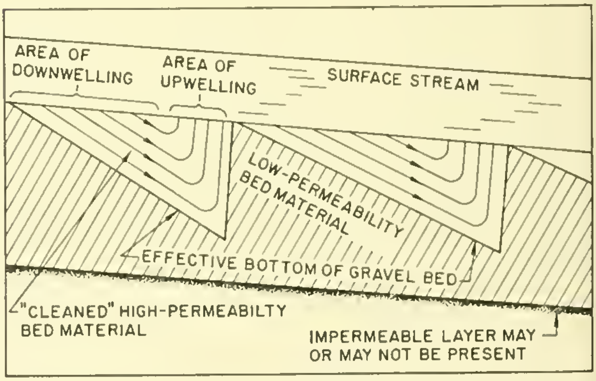
AREA OF DOWNWELLING
AREA OF UPWELLING
SURFACE STREAM
LOW-PERMEABILITY BED MATERIAL
EFFECTIVE BOTTOM OF GRAVEL BED
"CLEANED" HIGH-PERMEABILTY BED MATERIAL
IMPERMEABLE LAYER MAY OR MAY NOT BE PRESENT

FIGURE 11.—Interchange induced by variation of depth of the streambed.

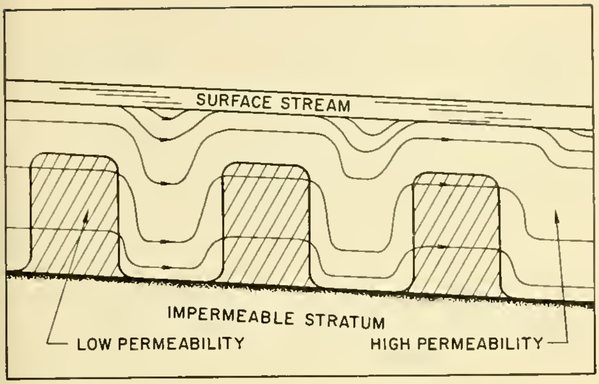

FIGURE 12.—Interchange induced by creating adjacent regions of high and low permeability.

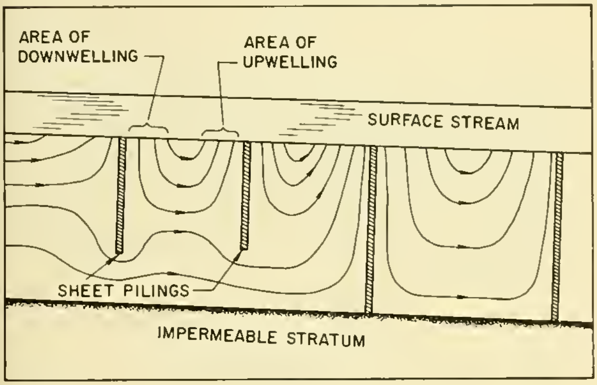

FIGURE 13.—Interchange induced by sheet pilings.

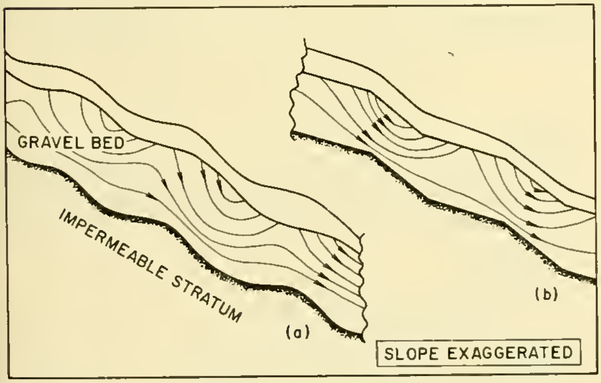

FIGURE 14.—Interchange established in streambeds by shaping the gravel bed into (a) a rounded profile and (b) an angular profile.

CONCLUSIONS

A constantly changing supply of well-oxygenated water is required in salmon spawning beds for proper survival, growth, and development of salmon embryos and alevins. Interchange between stream and intragravel water is essential for the delivery of adequate dissolved oxygen to preemergent fish. Knowledge of the factors that control interchange aids in understanding mortality factors and in developing means of increasing production of salmon fry from spawning beds.

TABLE 1.—*Summary of effects of permeability, depth, and surface profile of streambed on interchange*

Streambed characteristics	Causes upwelling	Causes downwelling	Illustrated in figure(s)
Bed depth, $b(x)$	Decreasing in the direction of flow.	Increasing in the direction of flow.	11.
Permeability, $k(x)$	do	do	12, 13.
Bed-surface profile, $y_1(x)$ (see fig. 2).	Concave	Convex	6, 7, 8.

Waterflow within a spawning bed can be described by Darcy's law and an equation of conservation of mass for an incompressible fluid. The potential causing intragravel flow,

$$\phi = y + g_c P/\rho g,$$

is the solution of the equation resulting from combination of Darcy's law and the mass conservation equation.

The potential along the stream-streambed boundary is described approximately by

$$\phi(x) = y_1(x) + \text{constant},$$

where $y_1(x)$ describes the profile of the streambed surface.

Interchange is controlled by the shape of the longitudinal profile of the streambed and longitudinal gradients of permeability and depth of the gravel bed according to the approximation

$$v_y \simeq \frac{Pg}{\mu} \frac{d}{dx}\left(kb\frac{dy_1}{dx}\right).$$

A concave streambed surface induces upwelling, and a convex surface induces downwelling. Increasing permeability of the streambed (measured in the direction of waterflow) induces downwelling, and decreasing permeability induces upwelling. Increasing bed depth (measured in the direction of waterflow) causes downwelling, and decreasing bed depth causes upwelling. The relation between direction of interchange and the shape of the streambed surface profile of the spawning bed was tested with an electrolytic-bath analog model and found to be correct.

The results of this work clearly demonstrate that the direction and magnitude of interchange in salmon spawning beds can be controlled by simple alteration of one or more of the three characteristics: (1) the surface profile of the bed, (2) the bed depth, and (3) the bed permeability. Selective removal of fine particles from "patches" of spawning gravel or the driving of impermeable sheet pilings could, for example, increase interchange and the amount of dissolved oxygen delivered to eggs and alevins.

NOTATION

Symbol	Notation	Units (Length, force, mass, time)
a	Length of reach of streambed.	L
b	Depth of streambed.	L
c_1, c_2	Constants of Ergun's equation.	FtL^{-4}
d	Stream depth.	L
g	Acceleration due to gravity.	Lt^{-2}
g_c	Newton's law constant, defined by force $=\frac{1}{g_c}$ mass $\times$ acceleration.	$MLF^{-1}t^{-2}$
Δh	Head loss.	L
$\mathbf{i}$	Unit vector in x direction.	
$\mathbf{j}$	Unit vector in y direction.	
$\mathbf{k}$	Unit vector in z direction.	
k	Permeability, a function of (x, y, z).	L^2
L	Length of permeameter.	L
n	Distance variable in direction normal to a surface.	L
N_{Re}	Reynold's number based on particle diameter.	
p	Parameter for adjusting boundary potential in equation (10).	Dimensionless
P	Pressure.	FL^{-2}
q	A positive adjustable parameter, (equation (13)).	Dimensionless
s	Distance variable along a streamline.	L
$U(x)$	Average stream velocity.	Lt^{-1}
v	Seepage velocity.	Lt^{-1}
w	Width of streambed.	L
x, y, z	Distance variables along axes.	L
y_1	Elevation of streambed surface.	L
y_2	Elevation of surface of impermeable stratum.	L
Z	Complex variable $=x+\sqrt{-1}\,y$.	
ζ	Complex variable in image plane.	
μ	Liquid viscosity.	$ML^{-1}t^{-1}$
ρ	Water density.	ML^{-3}
ϕ	Potential for intragravel flow.	L
$\phi(x)$	Potential at bed surface $=\phi[x, y, (x)]$.	L
	$\nabla=\mathbf{i}\frac{\partial}{\partial x}+\mathbf{j}\frac{\partial}{\partial y}+\mathbf{k}\frac{\partial}{\partial z}$, the gradient operator.	L^{-1}
	$\nabla^2=\frac{\partial^2}{\partial x^2}+\frac{\partial^2}{\partial y^2}+\frac{\partial^2}{\partial z^2}$, the laplacian operator.	L^{-2}

NOTES

Vectors are denoted by boldface letters, e.g., $\mathbf{v}$ is a velocity vector

$\equiv$ is read as "is defined as"

$\simeq$ is read as "approximately equal to"

Δ is read as "the change in"

A vertical bar is read as "evaluated at," e.g.,$\big|_{y=b}$ = "evaluated at $y=b$"

$\propto$ is read as "is proportional to"

ACKNOWLEDGMENTS

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MORTALITY RATES IN POPULATIONS OF PINK SHRIMP, *PENAEUS DUORARUM*, ON THE SANIBEL AND TORTUGAS GROUNDS, FLORIDA[1]

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ABSTRACT

Mark-recovery experiments were made to obtain estimates of fishing and natural mortalities as a portion of studies related to the life history of commercial shrimps in the Gulf of Mexico. In two experiments, groups of pink shrimp were injected with biological stains and released into the Sanibel and Tortugas fisheries off the southwest coast of Florida. Marked shrimp were recaptured by commercial shrimp fishermen.

Mortality estimates were derived from analysis of marked shrimp recoveries during the first 10 and 8 weeks of the Sanibel and Tortugas experiments, respectively. In the Sanibel population, fishing mortality was estimated to have been 6.8 percent for each 2-week period, and all other losses in the population were 14.8 percent; for the Tortugas population, fishing mortality was estimated to have been 13.1 percent for each 2-week period, and all other losses 19.7 percent.

In the past 3 decades, biologists have probed at various aspects of the life histories of commercial shrimps in the Gulf of Mexico. Recently, large-scale, mark-recovery experiments were made to estimate rates of fishing and natural mortalities in shrimp populations. A mark-recovery experiment, in which biological stains were the marking agent, was undertaken on the Tortugas pink shrimp (*Penaeus duorarum*) trawling grounds west of Key West, Fla., in September 1961. Development of an appropriate recovery system brought return of 21.1 percent of the marked shrimp. These shrimp were in commercial catches and returned by fishermen at shrimp landing ports. Analysis of data produced estimates of the rate of fishing and natural mortality in the Tortugas pink shrimp population (Kutkuhn, 1966). Two similar experiments were carried out in south Florida waters in 1962 and 1963. Emphasis was placed on obtaining a complete tabulation of fishing effort and recovering a high percentage of the marked shrimp that were recaptured by commercial gear. One experiment was on the Sanibel grounds south of Sanibel Island, and the other on the Tortugas grounds (fig. 1). These two experiments form the basis of this report.

THE SANIBEL AND TORTUGAS FISHERIES

In both fisheries, trawling gear is similar to that used elsewhere in the Gulf of Mexico (Bullis, 1951). Trawling is at night because pink shrimp usually remain buried during the day. Other species of penaeid shrimp in the catches are of minor commercial importance.

The area known as the Sanibel grounds comprises about 2,000 km.^{2} (600 square nautical miles) of trawlable bottom in two sections south and northwest of Sanibel Island, Fla. Most fishing is on the southern portion of the grounds between the 11- and 18-m. depths. The fishery began in 1954 and has produced about 272,000 kg. (600,000 pounds) (tails) of pink shrimp annually. Peak catches are made from March through May each year when 35 to 90 vessels participate in the

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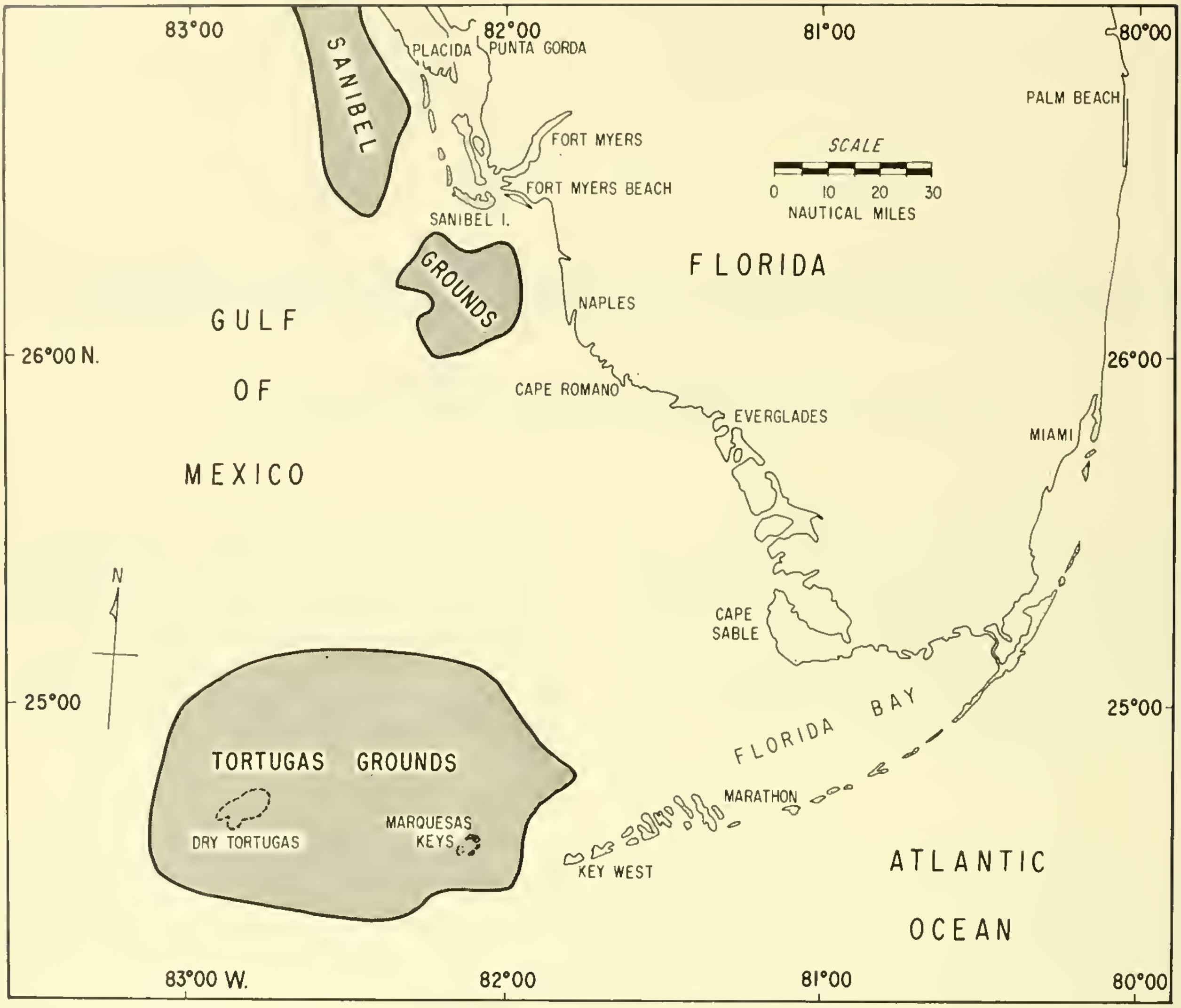
83°00
82°00
81°00
80°00
SANIBEL
PLACIDA
PUNTA GORDA
FORT MYERS
FORT MYERS BEACH
SANIBEL I.
SCALE
0 10 20 30
NAUTICAL MILES
PALM BEACH
GROUNDS
FLORIDA
NAPLES
GULF
OF
MEXICO
26°00 N.
26°00
CAPE ROMANO
EVERGLADES
MIAMI
N
CAPE
SABLE
25°00
25°00
FLORIDA BAY
TORTUGAS GROUNDS
MARATHON
DRY TORTUGAS
MARQUESAS
KEYS
KEY WEST
ATLANTIC
OCEAN
83°00 W.
82°00
81°00
80°00

FIGURE 1.—Geographic location of the Sanibel and Tortugas pink shrimp trawling grounds.

fishery. A few vessels trawl in the area throughout the year. Catches are landed at Fort Myers, Fort Myers Beach, Punta Gorda, Placida, or Naples, Fla.

The Tortugas grounds comprise about 10,000 km.^{2} (3,000 square nautical miles) of trawlable bottom west of Key West, Fla. Most fishing is between the 18- and 55-m. depths. The fishery began in 1950 and has produced about 5,442,000 kg. (tails) of pink shrimp annually. Peak catches occur from October through March each year, and 300 to 500 vessels participate in the fishery (Iversen and Idyll, 1959). Some trawling occurs on the Tortugas grounds throughout the year. Catches are landed at Key West, Marathon, Everglades, Fort Myers, Fort Myers Beach, or Tampa, Fla.

DATA REQUIREMENTS AND DESIGN OF EXPERIMENTS

To obtain the information required to estimate mortality rates, a group of animals is drawn from the standing crop, marked, and returned to the former environment. We assume that subsequent observations of the marked group are applicable to the population of which the group is believed to be part. Requirements for a successful experiment are that: (1) the experimental animals either are unaffected by the capture-mark-release process, or the effect is accurately measured and considered in the subsequent analyses; (2) accurate records are obtained of the numbers, dates, and locations of recaptures; and (3) a comprehensive tabulation is obtained of fishing effort in the area where the experimental group is available.

Experiments reported by Costello and Allen (1962) and Zein-Eldin and Klima (1965) indicate marking with biological dyes has little effect on the individual shrimp. Experience gained during earlier work (Costello and Allen, 1966) allowed the capture-release phases to be carried out with negligible injury to the live animals.

Personnel stationed at principal landing ports obtained recovery information on marked shrimp from fishermen and packing plant workers. In addition, they interviewed shrimp-boat captains to determine the time, location, and extent of fishing effort. We have a record of fishing effort for all shrimp vessels trawling in the Sanibel area. We have information on 77 percent of the shrimp vessels fishing the Tortugas grounds; and from these data we have estimated the effort that applied to the area containing marked shrimp.

FIELD OPERATIONS

To arouse their interest in the experiments, shrimp fishermen were contacted individually before the release of marked pink shrimp on the Sanibel and Tortugas grounds. A reward of $2.00 was offered for return of each marked shrimp.

In both areas, the Bureau of Commercial Fisheries chartered vessel *Silver Bay* captured shrimp and served as a platform for marking. Shrimp captured on the Sanibel grounds March 19 to 22, 1962, were stain-marked by injection of a 0.5 percent solution of fast green FCF, and 2,496 individuals were released at 26 randomly selected sites in the trawling area (fig. 2). Shrimp captured on the Tortugas grounds December 8 to 15, 1962, were stain-marked with a 0.25 percent solution of Trypan blue, and 2,350 individuals were released at 16 randomly selected sites in an area being fished by most of the fleet at that time (fig. 2).

Size compositions of marked shrimp released in both experiments, as determined from samples of marked shrimp ready for release, are shown in figures 3 and 4.

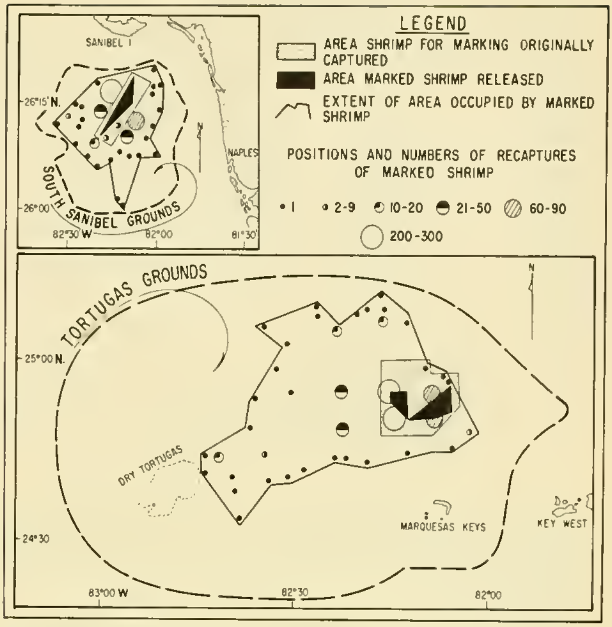
LEGEND
AREA SHRIMP FOR MARKING ORIGINALLY CAPTURED
AREA MARKED SHRIMP RELEASED
EXTENT OF AREA OCCUPIED BY MARKED SHRIMP
POSITIONS AND NUMBERS OF RECAPTURES OF MARKED SHRIMP
• 1
2-9
10-20
21-50
60-90
200-300
SANIBEL I
NAPLES
26°15'N.
26°00'
82°30'W
82°00
81°30'
SOUTH SANIBEL GROUNDS
TORTUGAS GROUNDS
N
25°00'N.
24°30
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
83°00'W
82°30
82°00

FIGURE 2.—Capture, release, and recapture areas of marked pink shrimp on the south Sanibel and the Tortugas grounds.

Adult pink shrimp, usually benthic, are particularly vulnerable to predation in the upper water layers, so an underwater release device described by Costello (1964) was used to lower and release marked shrimp near the bottom.

On the Sanibel grounds, 563 marked shrimp or 22.5 percent of the experimental population had been recovered by August 30, 1962. On the Tortugas grounds, 784 marked shrimp or 33.3 percent of those released had been recovered by March 29, 1963.

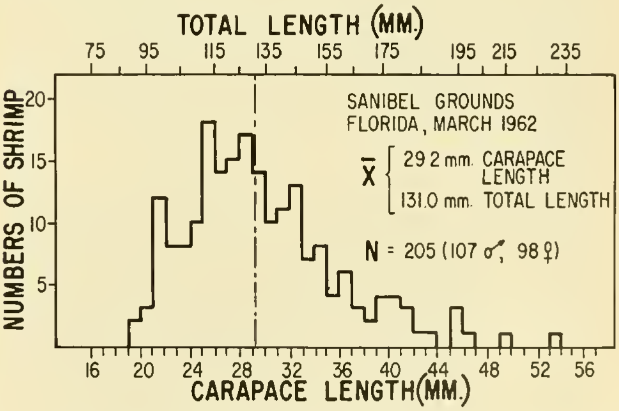

FIGURE 3.—Size composition of a random sample from the marked pink shrimp released on the south Sanibel grounds.

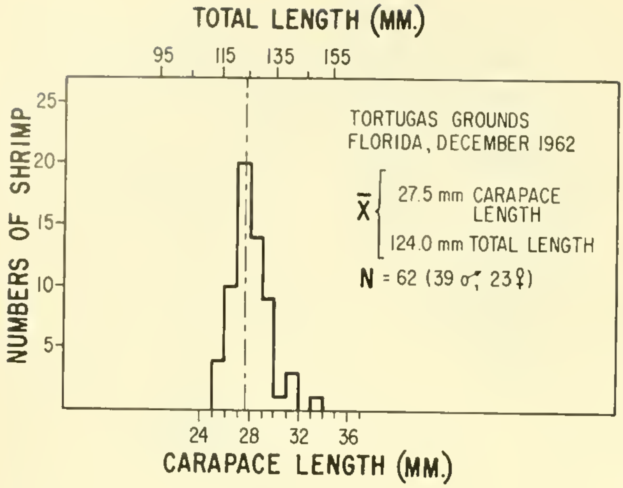

Figure 4.—Size composition of a random sample from the marked pink shrimp released on the Tortugas grounds.

DISPERSION OF THE MARKED SHRIMP

On both fishing grounds, plots of the positions of release and recapture of marked shrimp showed that: (1) some marked shrimp dispersed following release and (2) others remained within the immediate area of release for at least 10 weeks.

We used the release and recapture positions in both experiments to define the areas containing the marked shrimp. The outermost positions where marked shrimp were released were plotted and joined to enclose the original areas occupied; as recoveries were received, the outermost recapture positions were joined to delineate the expanding areas occupied. Definitions of the successive areas occupied were obtained with accumulation of several days' recoveries. The location of fishing effort was best established within an area from information compiled for 2-week intervals. For this reason, we selected 2-week intervals as most satisfactory.

Dispersion of marked shrimp from the original release areas proceeded at varying rates (figs. 5 and 6). Movements of the experimental group at Sanibel were generally toward the west and southwest. At Tortugas, dispersion was to the west and northwest. The outlined areas achieved midway between the first and last day of each succeeding 2-week period were selected as best descriptive of the average situation in the periods. At Tortugas, for example, the area occupied by marked shrimp at the midpoint of the first 2-week period after release was 961 km.^{2} (280 square nautical miles). The area occupied by marked shrimp any day of that 2-week period was considered, therefore, to be 961 km.^{2} (fig. 6). The outlines shown (figs. 5 and 6) and information from interviews on the location of fishing vessels enabled us to separate fishing effort expended in the area containing the experimental group of marked shrimp from total fishing effort on the grounds. During Period 1, in the Sanibel experiment, for example, the total effort expended on the grounds on March 31, 1962, was 16 boat-nights; the effort applicable to the experimental population was 6 boat-nights (table 1).

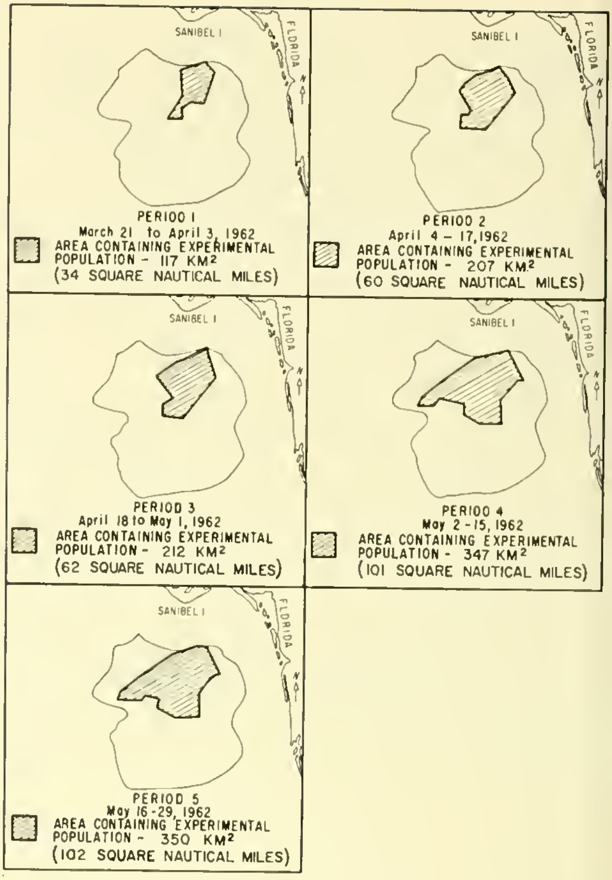
SANIBEL I
FLORIDA
PERIOD 1
March 21 to April 3, 1962
AREA CONTAINING EXPERIMENTAL POPULATION - 117 KM²
(34 SQUARE NAUTICAL MILES)
PERIOD 2
April 4 - 17, 1962
AREA CONTAINING EXPERIMENTAL POPULATION - 207 KM²
(60 SQUARE NAUTICAL MILES)
PERIOD 3
April 18 to May 1, 1962
AREA CONTAINING EXPERIMENTAL POPULATION - 212 KM²
(62 SQUARE NAUTICAL MILES)
PERIOD 4
May 2 - 15, 1962
AREA CONTAINING EXPERIMENTAL POPULATION - 347 KM²
(101 SQUARE NAUTICAL MILES)
PERIOD 5
May 16 - 29, 1962
AREA CONTAINING EXPERIMENTAL POPULATION - 350 KM²
(102 SQUARE NAUTICAL MILES)

Figure 5.—South Sanibel grounds. Area occupied by the population of marked pink shrimp in successive 2-week periods, as determined from recapture locations.

Description of the expanding area occupied by the marked shrimp permitted a refinement of the original data. For each 2-week period, a factor based on the relative size of the original area and the expanded area was computed. This factor

TABLE 1.—*Fishing effort and recoveries of stain-marked shrimp, south Sanibel grounds, March 21 to May 29, 1962*

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., boat-nights per 117 km.^{2} (34 square nautical miles)]	Recoveries
Period 1	*Boat-nights*	*Boat-nights*	*Km.^{2}*			*Number*
March 21	4	4	117	1.00	4.00	1
22	2	2	117	1.00	2.00	1
23	1	0	117	1.00	.00	0
24	0	0	117	1.00	.00	0
25	0	0	117	1.00	.00	0
26	0	0	117	1.00	.00	0
27	1	1	117	1.00	1.00	11
28	5	4	117	1.00	4.00	20
29	16	6	117	1.00	6.00	29
30	17	8	117	1.00	8.00	29
31	16	6	117	1.00	6.00	13
April 1	16	6	117	1.00	6.00	31
2	6	3	117	1.00	3.00	0
3	8	4	117	1.00	4.00	0
Period 2						
April 4	8	6	207	0.567	3.40	4
5	7	5	207	.567	2.84	3
6	5	3	207	.567	1.70	0
7	6	3	207	.567	1.70	2
8	12	9	207	.567	5.10	37
9	13	9	207	.567	5.10	43
10	17	11	207	.567	6.24	16
11	16	10	207	.567	5.67	29
12	13	9	207	.567	5.10	27
13	10	7	207	.567	3.97	0
14	2	1	207	.567	.57	2
15	3	2	207	.567	1.13	2
16	0	0	207	.567	.00	0
17	0	0	207	.567	.00	0
Period 3						
April 18	3	2	212	0.548	1.10	3
19	2	1	212	.548	.55	0
20	0	0	212	.548	.00	0
21	0	0	212	.548	.00	0
22	1	0	212	.548	.00	0
23	6	4	212	.548	2.19	0
24	6	4	212	.548	2.19	5
25	15	11	212	.548	6.03	14
26	17	13	212	.548	7.12	21
27	19	10	212	.548	5.48	5
28	15	9	212	.548	4.93	8
29	16	9	212	.548	4.93	1
30	17	9	212	.548	4.93	5
May 1	12	8	212	.548	4.38	5
Period 4						
May 2	13	8	347	0.337	2.70	3
3	7	4	347	.337	1.35	3
4	11	8	347	.337	2.70	4
5	12	11	347	.337	3.71	13
6	14	11	347	.337	3.71	9
7	13	13	347	.337	4.38	10
8	16	15	347	.337	5.06	5
9	19	19	347	.337	6.40	5
10	17	17	347	.337	5.73	11
11	17	18	347	.337	6.07	6
12	16	16	347	.337	5.39	6
13	16	16	347	.337	5.39	4
14	7	7	347	.337	2.36	3
15	1	1	347	.337	.33	0
Period 5						
May 16	1	1	350	0.333	0.33	0
17	1	1	350	.333	.33	0
18	1	1	350	.333	.33	0
19	4	4	350	.333	1.33	0
20	6	6	350	.333	2.00	0
21	10	10	350	.333	3.33	1
22	12	12	350	.333	4.00	16
23	21	11	350	.333	3.66	15
24	11	11	350	.333	3.66	2
25	10	11	350	.333	3.66	7
26	12	12	350	.333	4.00	2
27	15	15	350	.333	5.00	11
28	16	14	350	.333	4.66	4
29	20	19	350	.333	6.33	8

allowed measures of fishing effort to be converted to fishing intensity, i.e., fishing effort per unit area, the form required for subsequent analyses (tables 1 and 2).

ASSUMPTIONS AND JUSTIFICATIONS IN THE ESTIMATION OF MORTALITY

Any analytical approach to estimate mortality from mark-recapture data requires certain assumptions. Those we made are listed below followed by the evidence available to justify each.

Assumption 1:

Negligible losses of marked shrimp due to marking, handling at release, or to loss of marks after release.

Justification:

Experiments on survival of shrimp reported by Costello and Allen (1962) indicate that stain-marked shrimp have almost the same mortality as unmarked shrimp even in the presence of predators. Evidence of the longevity of stain marks (Dawson, 1957) excludes the likelihood that the marks fade or are lost over the period of the present experiments. Shrimp were examined individually before release to be certain that marks were distinct.

TABLE 2.—*Fishing effort and recoveries of stain-marked shrimp, Tortugas grounds, December 14, 1962 to February 7, 1963*

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., hours per 961 km.^{2} (280 square nautical miles)]	Recoveries
Period 1	*Hours*	*Hours*	*Km.^{2}*			*Number*
December 14	1,466	542	961	1.00	542	8
15	3,025	1,376	961	1.00	1,376	27
16	3,607	1,499	961	1.00	1,499	15
17	3,615	1,346	961	1.00	1,346	33
18	3,221	1,153	961	1.00	1,153	61
19	2,914	725	961	1.00	725	93
20	2,380	522	961	1.00	522	32
21	1,822	619	961	1.00	619	20
22	1,021	493	961	1.00	493	5
23	868	538	961	1.00	538	0
24	891	566	961	1.00	566	0
25	1,160	704	961	1.00	704	2
26	1,592	786	961	1.00	786	5
27	1,958	931	961	1.00	931	11
Period 2						
December 28	2,550	1,492	1,772	0.543	810	20
29	2,556	1,496	1,772	.543	812	17
30	1,360	830	1,772	.543	451	3
31	1,196	689	1,772	.543	374	0
January 1	1,175	713	1,772	.543	387	4
2	1,620	1,130	1,772	.543	613	11
3	2,158	1,502	1,772	.543	815	10
4	2,095	1,332	1,772	.543	723	11
5	2,607	1,787	1,772	.543	970	39
6	2,792	1,628	1,772	.543	884	43
7	1,044	545	1,772	.543	296	8
8	923	627	1,772	.543	340	4
9	1,809	1,397	1,772	.543	758	25
10	2,808	2,215	1,772	.543	1,202	18

TABLE 2.—*Fishing effort and recoveries of stain-marked shrimp, Tortugas grounds, December 14, 1962 to February 7, 1963*—Continued

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., hours per 961 km.^{2} (280 square nautical miles)]	Recoveries
Period 3	*Hours*	*Hours*	*Km.^{2}*			*Number*
January 11	3,209	2,432	2,162	0.444	1,080	19
12	3,202	2,414	2,162	.444	1,072	20
13	2,955	2,120	2,162	.444	941	11
14	1,709	983	2,162	.444	436	8
15	1,729	1,135	2,162	.444	504	7
16	1,561	1,205	2,162	.444	535	6
17	2,542	1,694	2,162	.444	752	10
18	3,039	1,887	2,162	.444	838	17
19	3,143	2,126	2,162	.444	944	23
20	3,085	1,976	2,162	.444	877	10
21	844	415	2,162	.444	184	1
22	663	345	2,162	.444	153	0
23	1,882	1,268	2,162	.444	563	4
24	749	483	2,162	.444	214	1
Period 4						
January 25	1,093	897	2,637 (768)	0.365	327	1
26	2,698	2,292	2,637	.365	837	23
27	2,973	2,390	2,637	.365	872	9
28	1,835	1,377	2,637	.365	503	5
29	1,617	921	2,637	.365	336	1
30	2,782	2,116	2,637	.365	772	3
31	3,118	2,630	2,637	.365	960	10
February 1	3,289	2,743	2,637	.365	1,000	4
2	3,185	2,461	2,637	.365	898	5
3	1,843	1,291	2,637	.365	471	4
4	580	236	2,637	.365	86	1
5	488	238	2,637	.365	87	0
6	773	319	2,637	.365	116	0
7	1,095	621	2,637	.365	227	1

Assumption 2:

No losses due to predation during release.

Justification:

The experimental groups, as noted earlier, were returned to the bottom in a release box designed to avoid predation. The effectiveness of this release device had been demonstrated previously by underwater observations (Rounsefell, 1963).

Assumption 3:

Negligible loss of recaptured marked shrimp because of failure to detect them in the commercial catch or failure to report them.

Justification:

Assurance that a high percentage of recaptures were recognized and returned (recovered) was given by the following evidence:

a. Just before these experiments, most fishermen and processing-plant personnel in the area were shown samples of stain-marked shrimp.

b. Eight experiments with stain-marking had been performed recently in these areas, and most fishermen and processing-plant personnel in the Sanibel and Tortugas areas were familiar with stain-marked shrimp.

c. A reward was paid for each recovery when vessels arrived in port or as soon as marked shrimp were found in a processing plant.

d. During both experiments, marked shrimp had many chances to be recognized and returned because all shrimp were "headed" by hand. All Sanibel shrimp were headed at sea, but some Tortugas catches were headed ashore. Ordinarily, a single fisherman may remove heads from 8,000 or more shrimp in a single night. During the Sanibel experiment, fishermen, two to a boat, removed the heads from an average of only about 4,000 shrimp each night (table 3). When they handled less than their capacity, fishermen had time to examine each shrimp and recognize the marked animals. Considerably more shrimp were handled per night by Tortugas fishermen than by Sanibel fishermen. Crew members from many boats told us, however, that they spread catches of shrimp on the deck before heading so that marked shrimp might be easily noticed. Most of the total recoveries (93 percent) were recognized by fishermen at sea and removed from the catch before the return to port (Allen and Costello, 1966). Ashore, Bureau personnel daily reminded workers in processing plants to watch for marked shrimp that passed unnoticed by fishermen at sea.

e. "Planting" experiments indicated a high ratio of recoveries to recaptures. During the time marked shrimp occurred in commercial catches from the Tortugas grounds, small numbers were placed secretly in catches of whole shrimp being unloaded at shore processing plants. These shrimp were of identical size and were

TABLE 3.—*Fishing effort and pink shrimp catch (individuals), south Sanibel grounds, March to May 1962* [1]

Period	Fishing effort	Total shrimp catch [2]	Number of shrimp caught per boat-night [2]
	Boat-nights	*Number*	*Average*
3/21–27	8	24,000	3,000
3/28–4/3	84	403,000	5,000
4/4–10	68	345,000	5,000
4/11–17	44	212,000	5,000
4/18–24	18	45,000	3,000
4/25–5/1	111	434,000	4,000
5/2–8	86	358,000	4,000
5/9–15	93	341,000	4,000
5/16–22	35	105,000	3,000
5/23–29	105	300,000	3,000
Mean catch per boat per night			4,000

[1] Based on 171 interviews of boats landing shrimp at Fort Myers and Fort Myers Beach. Compiled by Bureau of Commercial Fisheries Branch of Statistics.

[2] Rounded to the nearest thousand.

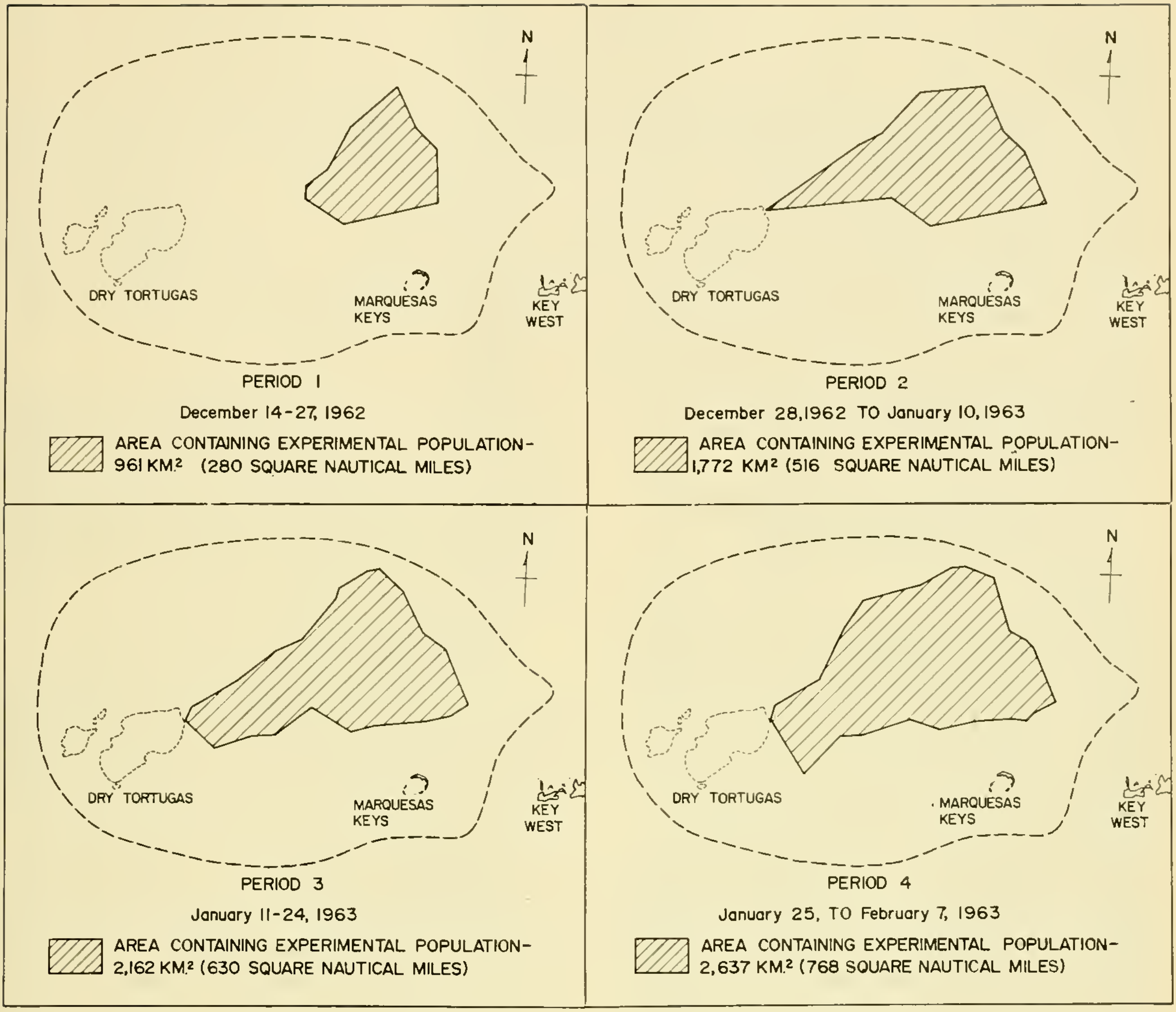
N
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
PERIOD 1
December 14-27, 1962
AREA CONTAINING EXPERIMENTAL POPULATION-961 KM.² (280 SQUARE NAUTICAL MILES)
N
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
PERIOD 2
December 28, 1962 TO January 10, 1963
AREA CONTAINING EXPERIMENTAL POPULATION-1,772 KM² (516 SQUARE NAUTICAL MILES)
N
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
PERIOD 3
January 11-24, 1963
AREA CONTAINING EXPERIMENTAL POPULATION-2,162 KM.² (630 SQUARE NAUTICAL MILES)
N
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
PERIOD 4
January 25, TO February 7, 1963
AREA CONTAINING EXPERIMENTAL POPULATION-2,637 KM.² (768 SQUARE NAUTICAL MILES)

FIGURE 6.—Tortugas grounds. Area occupied by the population of marked pink shrimp in successive 2-week periods as determined from recapture locations.

stained similarly to those released on the fishing grounds. A second mark, not visible to processing plant personnel, was placed on these "planted" specimens so that we could distinguish them from genuine recoveries. Results of these and of later similar experiments indicated that 75 to 89 percent of marked shrimp which enter the shore processing plants are recovered.

We have no direct measure of the percentage of marked shrimp recovered from those headed at sea. In similar mark-recovery experiments in the northern Gulf of Mexico, however, Klima and Benigno (1965) estimated that 83 percent of recaptured marked shrimp were recovered on shrimp boats and 14 percent were recovered in processing plants. They concluded, therefore, that only 3 percent were entirely overlooked.

Assumption 4:

If losses did occur, the ratio of undetected recaptures to recoveries did not change during the periods used in analyses.

Justification:

Field personnel concluded, from daily interviews, that interest in recovering marked shrimp aboard shrimp boats and in processing plants remained constant for at least the first 10 weeks of both experiments. Marked shrimp were recovered over extended periods of time, but recovery and fishing-effort information collected only within the first 10 weeks following release of the marked animals was used for estimating mortality rates for the Sanibel and Tortugas experiments. The period was so restricted because recoveries of marked shrimp reflect their relative abundance in the commercial catch only as long as the interest in recovering them remains constant. The reward is a prime inducement for the return of marked shrimp. Reasonably, when the number of marked shrimp in catches drops markedly, interest wanes and an increasing percentage of recaptures may pass through the fishery unnoticed.

THEORETICAL AND BIOLOGICAL CONSIDERATIONS

Fundamental tenets in computation of mortality estimates are that the decline in numbers in an animal population follows an exponential trend, and that a constant instantaneous mortality coefficient is operative. The latter concept has been applied to many animal populations. Presumably, it may be applied to shrimp. Paulik (1963) noted the acceptability of this concept in short-term experiments, as are being considered here.

Mortality estimates are derived from mark-recovery experiments by measuring density changes in an experimental population. In this application, otter trawls used by the commercial shrimp fleet serve as sampling gear, and decreases in density are reflected in decreased catches of marked shrimp per unit fishing intensity. The average rate of loss is computed and expressed numerically as the instantaneous total mortality coefficient.

At this point, it is pertinent to offer possible explanations for the fluctuations in recoveries of marked shrimp per unit fishing intensity on the Sanibel grounds (table 4), but not on the Tortugas grounds (table 5). It appears, superficially, that decreases in the abundance of the marked shrimp from one time period to the next should be consistently reflected in decreased recaptures per unit fishing intensity. Increased recaptures of marked shrimp at a later time period appear to violate a basic premise upon which the estimate of mortality is based.

The reasons for this apparent anomaly are not entirely clear. Possible sources of bias in the interpretation of mark-recovery data may be introduced by: (1) nonuniform distribution of marked animals over the bottom and (2) inaccurate estimation of fishing effort in relation to the spatial distribution of marked animals. Such difficulties in interpretation of marking experiments were discussed by Ricker (1958).

These sources of bias, however, may not be the only causes of fluctuations in recovery of shrimp per unit fishing intensity. Allen, Delacy, and Gotshall (1960), Konstantinov (1964), Parrish, Blaxter, and Hall (1964), and others recognized that biological activities may affect the catchability of aquatic animals. Wathne (1963) and Fuss and Ogren (1966) noted variable burrowing habits of pink shrimp which may explain variations in shrimp availability to the trawl. Additionally, although pink shrimp are ordinarily benthic, we have frequently observed them in dense schools at or near the surface at night. Similar observations were reported by Burkenroad (1949), Higman (1952), Tabb, Dubrow, and Jones (1962), Iversen and Van Meter (1964), and Joyce (1965). Obviously, vertical movements of

Table 4.—*Fishing intensity and numbers of marked shrimp recovered, south Sanibel grounds, March 1962 to May 1962*

[$N_o=2{,}496$]

Recovery interval	Marked shrimp recovered	Applicable fishing effort	Area occupied by experimental population	Factor based on area occupied	Fishing intensity (effort per unit area)	Recoveries [1]	Natural logs of recoveries [1]
	Number	*Boat-nights*	*Km.*^{2}			*Number*	
3/21–4/3	135	44	117	1.00	44.0	139.9	4.94092
4/4–4/17	165	75	207	.567	42.5	177.0	5.17615
4/18–5/1	67	80	212	.548	43.8	69.8	4.24563
5/2–5/15	82	164	347	.337	55.3	67.6	4.21361
5/16–5/29	66	128	350	.333	42.6	70.6	4.25703
5/30–8/30 [2]	47						

[1] Per (mean) 45.6 boat-nights fishing intensity.

[2] Recoveries during this final period were not used in analysis.

TABLE 5.—*Fishing intensity and numbers of marked shrimp recovered, Tortugas grounds, December 1962 to February 1963*

[N=2,350 [1]]

Recovery interval	Marked shrimp recovery	Applicable fishing effort	Area occupied by experimental population	Factor based on area occupied	Fishing intensity (effort per unit area)	Recoveries [2]	Natural logs of recoveries [2]
	Number	*Thousand hours*	*Km.*^{2}			*Number*	
12/14–12/27	302	11.8	961	1.00	11.8	241.8	5.4881
12/28–1/10	213	17.4	1,772	0.543	9.4	214.1	5.3665
1/11–1/24	137	20.5	2,162	.444	9.1	142.2	4.9572
1/25–2/7	67	20.5	2,637	.365	7.5	84.4	4.4356
2/8–3/29 [3]	29	------------	------------	------------	------------	------------	------------

[1] In analysis, this number adjusted to 2,314 for the mean release date of 12/14/62.
[2] Per (mean) 9,450 hours of fishing intensity.
[3] Recoveries during this final period were not used in analysis.

shrimp in the water mass will affect their availability to a trawl fishing on or near the bottom.

Over short periods of time then, we may normally expect considerable variability in catches of pink shrimp (unmarked or marked) which is independent of the decrease in a population with time.

DEFINITIONS OF NOTATIONS

Notations and symbols suggested by Beverton and Holt (1957) and Holt (1960) are used in our analysis and summary. Definitions follow:

Z=Instantaneous total mortality coefficient
F=Instantaneous coefficient of mortality caused by fishing
M=Instantaneous coefficient of mortality by (natural) causes other than fishing
X=Instantaneous coefficient of other loss in marking theory, i.e., losses in the experimental population due to all causes except recapture (true natural mortality plus losses of individuals which for any reason become unavailable for recapture)[2]
f=Fishing intensity (fishing effort per unit area)
N_0=Initial size of the experimental population (number in batch of marked shrimp liberated at time zero)
n=Number of marked shrimp recaptured in a given period, e.g.,
n_1=Number in first period, n_2=Number in second period, etc.

ANALYSIS

Variations in catch per unit fishing intensity described previously do not nullify the value of this information in deriving mortality estimates. Population decreases with time during the experimental period are reflected well by these data. An analytical technique designed to yield mean instantaneous mortality coefficients, accordingly, was chosen.

The numbers of marked shrimp recaptured each 2-week period varied considerably in both experiments in response to fluctuating fishing intensity. As suggested by Kutkuhn (1966), the numbers of recoveries that accumulate each period may be corrected to unit fishing intensity and analytical methods given by Beverton and Holt (1957, pp. 185–191) applied. A factor of 45.6, the average number of boat-nights [3] of fishing intensity per 2-week period, was applied to Sanibel recoveries to convert them to a unit basis (table 4); a factor of 9,450, the average number of hours of fishing intensity per 2-week period, was used to convert the Tortugas recoveries (table 5). We recognize, however, that this method of analysis is better suited to the Tortugas experiment than to the Sanibel experiment where fishing intensity fluctuated considerably from period to period.

Lines fitted to the natural logarithms of adjusted recoveries (figs. 7 and 8) indicate that the decline in numbers of both experimental groups followed a linear trend. Regression lines have a slope equal to minus (F+X) or Z. For Z, the instantaneous total mortality coefficient, the regression equations yielded values of 0.233 for Sanibel and 0.357 for Tortugas. Values of 153.4 and 121.5 (designated n_1 and n_2) were obtained by substituting appropriate units of time in the regression equation for Sanibel. These figures are

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[2] As defined by Beverton and Holt (1957). Holt (1960) gave a varied meaning.

[3] Sanibel fishing effort was reported to us in boat-nights rather than in hours. No valid conversion factor was available to convert boat-nights to hours; therefore, Sanibel effort was used in the form of boat-nights as originally reported.

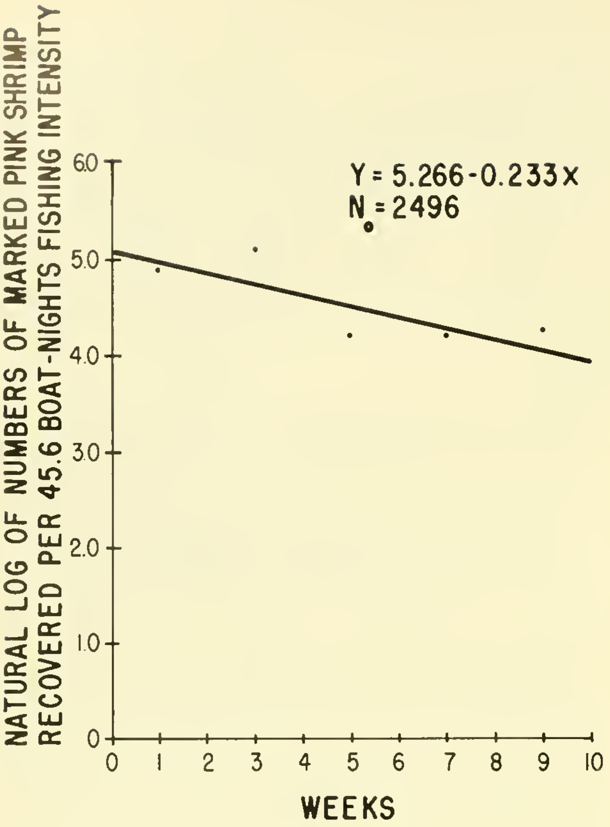

FIGURE 7.—Mortality of marked pink shrimp, south Sanibel grounds, March 21 to May 29, 1962.

the theoretical numbers of recoveries of marked shrimp that would have occurred in the first and second 2-week periods following release of the experimental population with fishing intensity constant at 45.6 boat-nights per 2-week period. For the Tortugas fishery, on the basis of 9,450 hours of fishing intensity per 2-week period, a like procedure gave values of 269.3 and 188.5 for n_1 and n_2. With these numerical values for n_1 and n_2, and the N_0 figures given in tables 4 and 5, we may enter the following expressions from Beverton and Holt (1957, p. 190).

$$F=\frac{\frac{n_1}{\tau}\log_e\left(\frac{n_1}{n_2}\right)}{N_o\left(1-\frac{n_2}{n_1}\right)}$$

$$X=\frac{1}{\tau}\left\{\log_e\left(\frac{n_1}{n_2}\right)\right\}\left\{1-\frac{n_1}{N_o\left(1-\frac{n_2}{n_1}\right)}\right\}$$

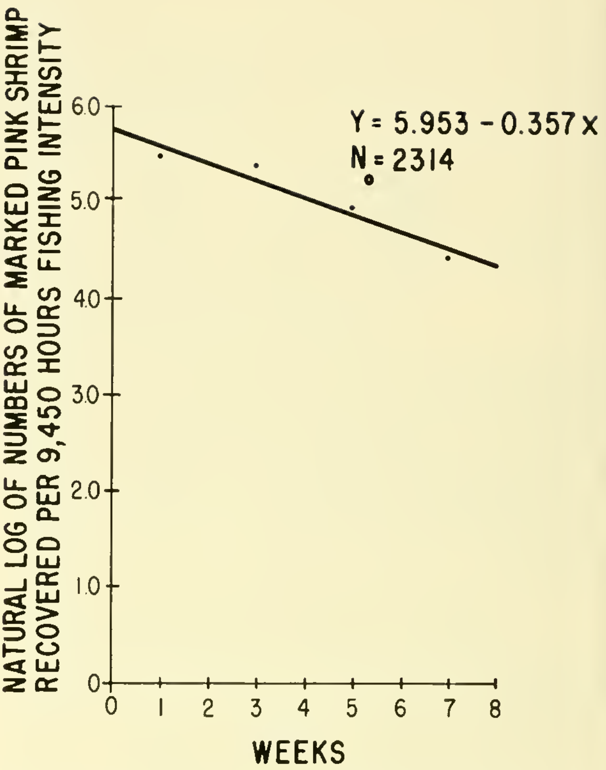

FIGURE 8.—Mortality of marked pink shrimp, Tortugas grounds, December 14, 1962, to February 7, 1963.

By application of these expressions, we divide the Z values given above into fishing mortality (F) and "other losses" components (X).

These calculations gave the following estimates:

	Mortality	Instantaneous rates	Rates (percent) per 2-week period
Sanibel	Fishing	0.0689	6.8
	Other	.1644	14.8
Tortugas	Fishing	.1385	13.1
	Other	.2185	19.7

SUMMARY

Mortality estimates for the Sanibel population have not been previously reported. For the Tortugas population, estimates derived here indicate mortality higher than was reported by Iversen (1962), but considerably lower than was calculated by Kutkuhn (1966).

In either the Sanibel or Tortugas experiment the values obtained for X (coefficient of other loss) cannot be readily accepted as estimates of

M (coefficient of true natural mortality). By definition, X includes M, together with losses from all other causes except fishing. Losses due to migration from the area of fishing, and mortality attributable to marking, handling, or the release procedure can contribute a considerable loss to the experimental group of animals. This fact must be given consideration in the use of X as an estimate of M.

Consideration of possible management implications calls for recognition that operation of trawls may have complex effects upon a resident shrimp population (Lindner, 1936). Also, cessation of trawling affects the population. The mortality estimates we have given were calculated from data assembled while a sizable fishery was in progress. The coefficient of true natural mortality may shift considerably when a regulatory measure, e.g., closure of the fishery, is applied.

F, as a function of fishing effort, fluctuates over short periods of time. The value of M also changes in response to such factors as varying predation by migratory schools of fish. The values derived here, however, for shrimp of the sizes in the experiment, may establish the approximate levels for offshore pink shrimp fisheries. These parameters, together with supplementary information and recommendations by Lindner (1966), may be used as a basis for management of the valuable Sanibel and Tortugas resources.

ACKNOWLEDGMENTS

The crew of the research vessel *Silver Bay* and management personnel of the south Florida shrimp industry helped with the field experiments.

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OCEANOGRAPHIC CONDITIONS IN THE NORTHEAST PACIFIC OCEAN AND THEIR RELATION TO THE ALBACORE FISHERY

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ABSTRACT

This paper describes initial environmental conditions encountered by albacore, *Thunnus alalunga* (Bonnaterre), in their annual entry to the region off the northwest coast of the United States, describes the physical mechanisms that produce these conditions, and indicates their influence on the highly variable number of albacore available to the fishery. The region studied extends from the coast of Oregon and Washington to long. 132° W. between lats. 41° N. and 48° N., within which the northernmost part of the American coastal fishery for albacore usually has been confined.

Upwelling, effects of runoff from land, and the excess of precipitation over evaporation produce annually recurrent patterns of distribution of variables. This recurrent aspect is used to distinguish three spatial provinces above and two provinces below the main halocline, each of which reflects the balance of processes affecting it. Variations in the distributions of variables from year to year are shown to be attributable to changes in wind field, in fresh-water discharge from land, and in advection. These variations do not, however, obscure the basic patterns generated by dominant processes.

The distribution of available albacore over the study area is inferred to be sensitive to spatial and year-to-year differences in temperature and in salinity. Higher temperatures, produced by greater retention of heat in the surface layer of the province dominated by effects of land runoff, may give rise to greater concentrations of albacore in this province. Salinity, to which temperature is inversely related, may control the degree to which spatial temperature differences can be effective, possibly by its influence on osmotic pressure. If future investigation confirms this hypothesis, success of the fishery will be predictable from preseason information on wind field, geostrophic flow, and Columbia River discharge.

The yield of the seasonal fishery for albacore (*Thunnus alalunga*) off Oregon and Washington is characteristically variable. Within the period 1951–64, annual landings in these States ranged from 0.6 to 13.5 million pounds. Nearly all albacore landed in Oregon and Washington in 1954 and 1955 were caught south of lat. 40° N.; consequently, the northern fishery was considered to have failed completely in these years.

The region off the Oregon-Washington coast usually represents the northernmost end of the range within which commercially harvestable concentrations of albacore have been found along the North American coast. The fishery spans a shorter time interval than that to the south, perhaps because environmental conditions are tolerable to albacore for a shorter time. Fishing usually begins there in mid-July, attains a maximum effort and catch in late August and September, and largely ends by the end of October. The California fishery, by contrast, often starts a month earlier and ends a month later. Moreover, fishing intensity off Oregon and Washington is more sensitive to weather, to the price of albacore, and to diversion from tuna trolling to salmon fishing and bottom fishing than off California. Variation in the yield of albacore from the Oregon-Washington fishery cannot be assigned solely, however, to variation in fishing intensity, because the yield also depends on the fluctuations in availability of albacore in the region.

The number of fish available to a fishery at a particular time is often a complex function of abundance and behavior, both of which may be markedly affected by the environment. Influence of the environment upon albacore off Oregon and Washington has been detectable only through relations of sea temperatures to landings of the commercial fishery (Johnson, 1962) and to catches by Bureau vessels (Alverson, 1961). Water clarity, which varies largely with the concentration of particulate matter, also has been thought to affect albacore availability (Murphy, 1959); to date, however, this hypothesis has not been tested off the Oregon-Washington coast. Powell and Hildebrand (1950) noted a relationship of tuna catches with observed ocean conditions; albacore were

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caught in blue, warm water but not in green, cold coastal water. As they noted, however, this effect probably is attributable to temperature rather than to water color. Other environmental variables that have received attention as possible determinants of albacore availability and abundance (or density) include salinity and concentration of forage. No examples of observed relations of these factors to numbers of accessible albacore are available, however, and the relation of temperature to albacore was only grossly defined in previous studies.

The purposes of this paper are to describe the environment that albacore encounter when they first enter the region off the coast of Oregon-Washington, to suggest the physical mechanisms that produce these conditions, and to indicate which of these conditions appear to influence the number of albacore available to the fishery.

DATA SOURCES

Data from which distributions of variables were derived were collected in July 1961–64 on Cruises 51, 55, 60, and 66 of M/V *John N. Cobb*, a cooperative program with the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Seattle, Wash. (Owen, 1963, 1967a); in July 1961–62 on Cruises BB–290 and BB–310 of R/V *Brown Bear*, Department of Oceanography, University of Washington, Seattle; and in July 1963–64 on Cruises 6307 and 6407 of R/V *Acona*, Department of Oceanography, Oregon State University, Corvallis, Oreg. Data from which averages of catch per unit of effort for the commercial fishery were computed are from Ayers and Meehan (1963) and from James M. Meehan of the Fish Commission of Oregon (personal communication).

OCEANOGRAPHIC PROCESSES AND DISTRIBUTIONS OF VARIABLES

The study area (fig. 1) is part of the subarctic Pacific Ocean and hence exhibits its principal characteristics: dilution of the surface layers by excess of precipitation over evaporation; and presence of a well-defined, permanent halocline in which year-round temperatures are nearly identical with winter temperatures of the surface layers (fig. 2). The oceanography of the subarctic Pacific was reviewed by Uda (1963), and by Dodimead, Favorite, and Hirano (1963).

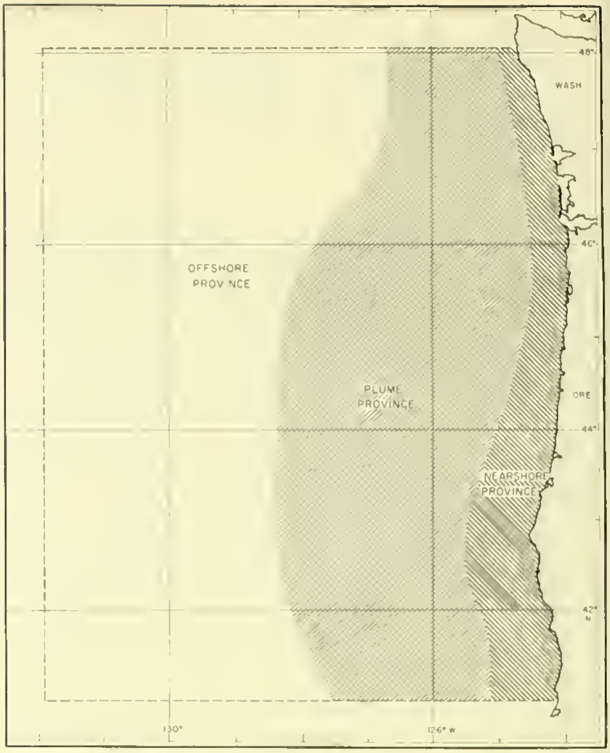

Figure 1.—Oceanographic provinces (schematic) off the Oregon-Washington coast in summer. Dashed line represents general limit of study area.

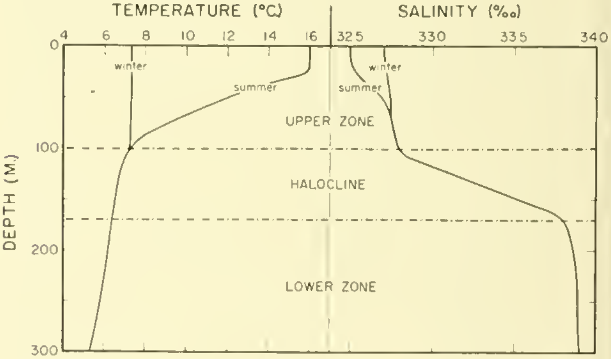

Figure 2.—Schematic diagram of vertical temperature and salinity structures in the eastern subarctic Pacific in summer and winter.

Processes that determine the distribution of salt and heat over the subarctic region combine in the study area with effects of nearshore upwelling, river discharge, and bottom topography to produce the distributions of variables reported here. Oceanography in part of the area was reviewed by Budinger, Coachman, and Barnes (1964), and an annotated bibliography on the area influenced by the Columbia River discharge was prepared by Anderson, Barnes, Budinger, Love, and McManus (1961). An atlas of July oceanographic conditions was prepared as a supplement to the present work by Owen (1967b).

RECURRENT FEATURES OF DISTRIBUTIONS OF VARIABLES

Both in the surface and deep layers, patterns of distribution of physical variables recur from summer to summer over the region off Oregon-Washington. This recurrent nature permits discussion of physical mechanisms that operate in the region.

Upper Zone

Above the main halocline (fig. 2) the area is divisible in summer into three meridionally bounded regions on the basis of physical processes believed to produce the distributions of variables characteristic of each. These regions may be termed nearshore province, plume province, and offshore province (fig. 1).

Nearshore Province.—The first subdivision, nearshore province, lies along the coast in summer as a band of cold, saline water about 50 nautical miles (90 km.) wide, interrupted only by fresher water from coastal sources. It is dominated by the effects of coastal upwelling. Intense horizontal gradients of temperature, salinity, density, and oxygen concentration are encountered from the sea surface to depths exceeding 250 m. (figs. 3, 4, 5, and 6). These gradients result from transformation of offshore vertical gradients, recognized there as the thermocline, halocline, pycnocline, and oxycline, into nearshore horizontal gradients by upwelling.

The offshore summer thermocline (fig. 7) does not coincide with the permanent halocline, but lies above it. Consequently, the corresponding horizontal temperature gradient of the nearshore regime lies farther from the coast than does the horizontal gradient associated with the permanent halocline (compare figs. 7 and 8). Once transported to the near-surface layer by upwelling, water of subsurface origin is warmed by local heat exchange across the sea surface. Because of this local heat gain neither temperature nor temperature gradient permits close assessment of intensity of upwelling, although both serve to indicate the offshore extent of upwelling influence.

The nearshore distribution of salinity is relatively uninfluenced by processes other than diffusion and upwelling in the nearshore province, except where dilution occurs near coastal sources of fresh water. The water of the offshore halocline is displaced upward within upwelling areas and usually reaches the surface layers. The inshore occurrence near the sea surface of water of the same salinity (33.8‰) as that at the bottom of the offshore halocline (fig. 8) indicates upward transport of water from depths below the permanent halocline. Diffusion and transport across surfaces of constant salinity near shore apparently are important; the near-surface horizontal gradient of salinity in this province is about three orders of magnitude less than the corresponding vertical gradient in the halocline offshore.

Distribution of mass in the nearshore province follows the pattern characteristic of coastal upwelling in general: large horizontal gradients of density are normal to the coastline in the upper layer (fig. 5), and vertical gradients of density are weak. Mass transport probably takes place across surfaces of constant density within the near-surface layers, however, because density is decreased locally there by net heat gain from insolation.

Oxygen concentration may exhibit significant local increase in upwelled water due to photosynthetic processes and to rapid exchange with atmospheric oxygen (fig. 6). These local changes are not sufficiently rapid, however, to obscure the effect of upwelling on oxygen concentration; low oxygen values that denote deep offshore origin are consistently present in surface layers of the nearshore province.

Water in the surface layers of the nearshore province is of deep offshore origin. Water of $\sigma_t \geq 26$, corresponding in density to water near the bottom of the offshore halocline (fig. 9), is common in the nearshore surface layers (fig. 5). The density of some of this water must have been decreased, however, by mixing in transit and by local heating; therefore, it must have come from depths in excess of that of the offshore halocline.

Plume Province.—The second subdivision, plume province, is characterized by near-surface water of low salinity, the result of dilution by coastal fresh water. The Oregon-Washington coast represents a variable line source of fresh water. The Columbia River, however, with a mean annual discharge of 7.3 x 10^3m.^{3} sec.$^{-1}$ and a maximum discharge (in June) of about 16.0 x 10^3m.^{3} sec.$^{-1}$, contributes more than 73 percent of the average

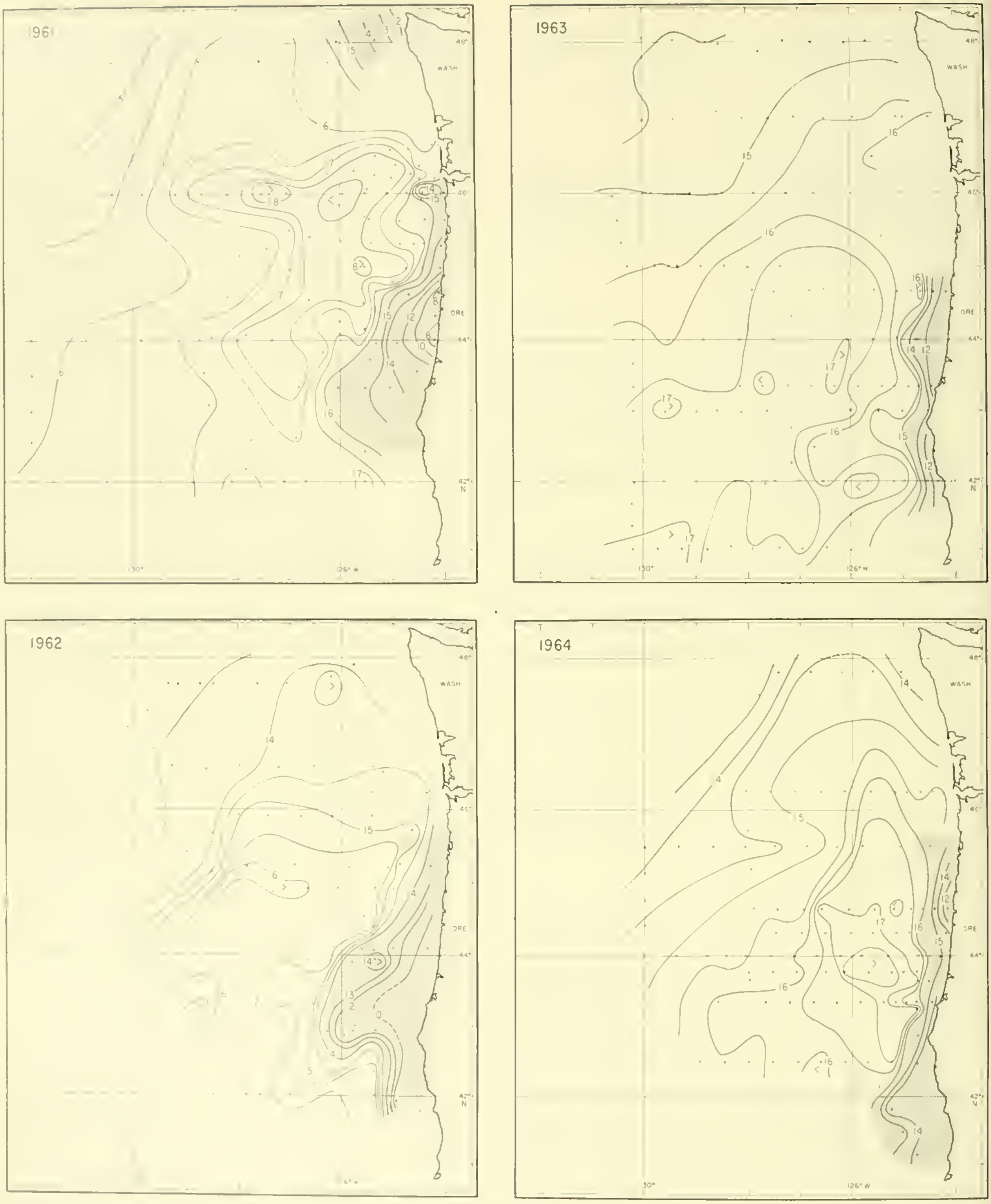
1961
1963
1962
1964
WASH
ORE
48°
46°
44°
42° N
130°
126° W
14
15
16
17
12

Figure 3.—July distribution of temperature at the sea surface, 1961–64. Contour interval is 0.5° C. except where shaded.

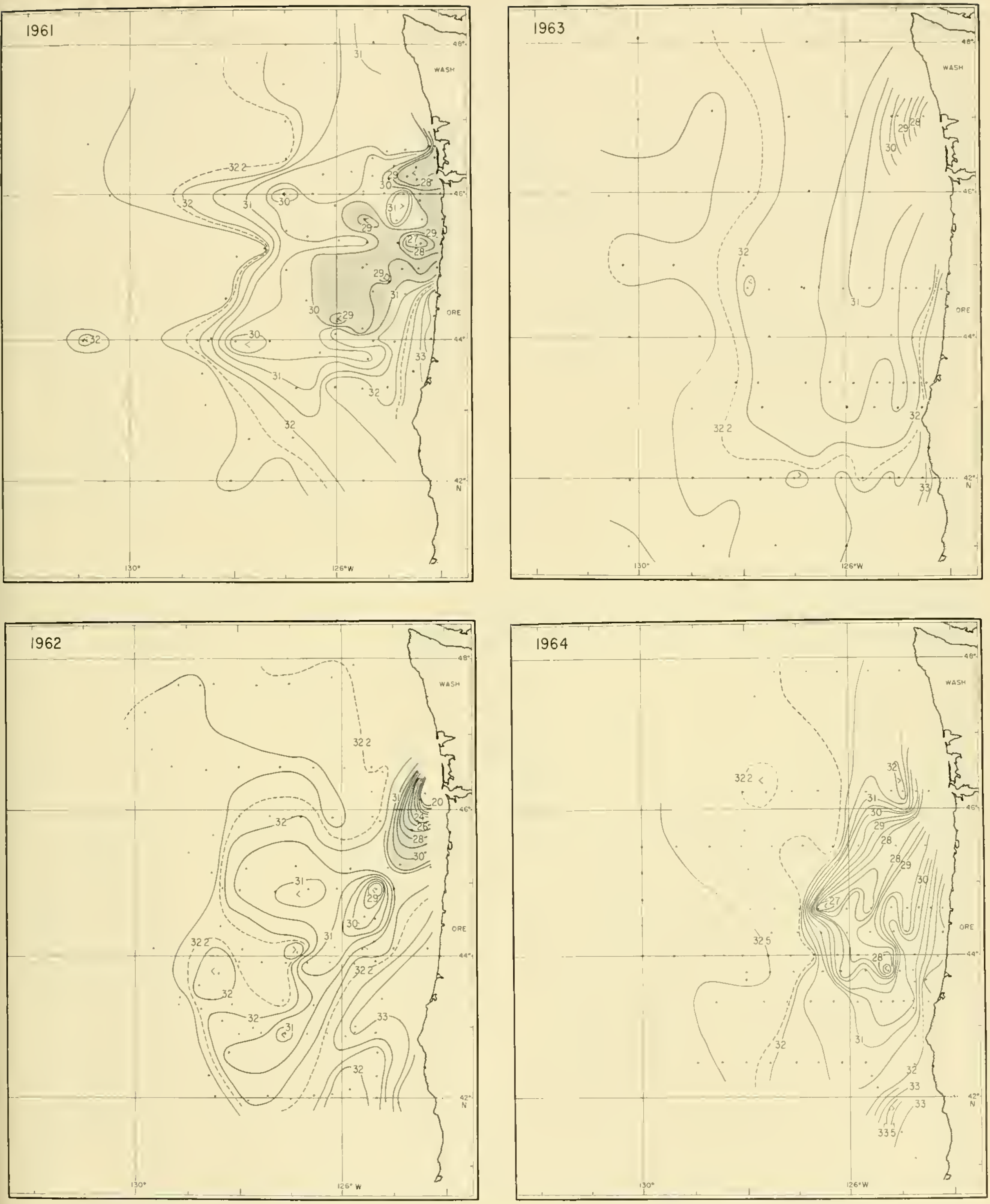
1961
1963
1962
1964
WASH
ORE
48°
46°
44°
42° N
130°
126°W
31
32
32.2
30
29
28
27
33
20
24
26
32.5
33.5

FIGURE 4.—July distribution of salinity at the sea surface, 1961–64. Contour interval is 0.5°/oo except where shaded.

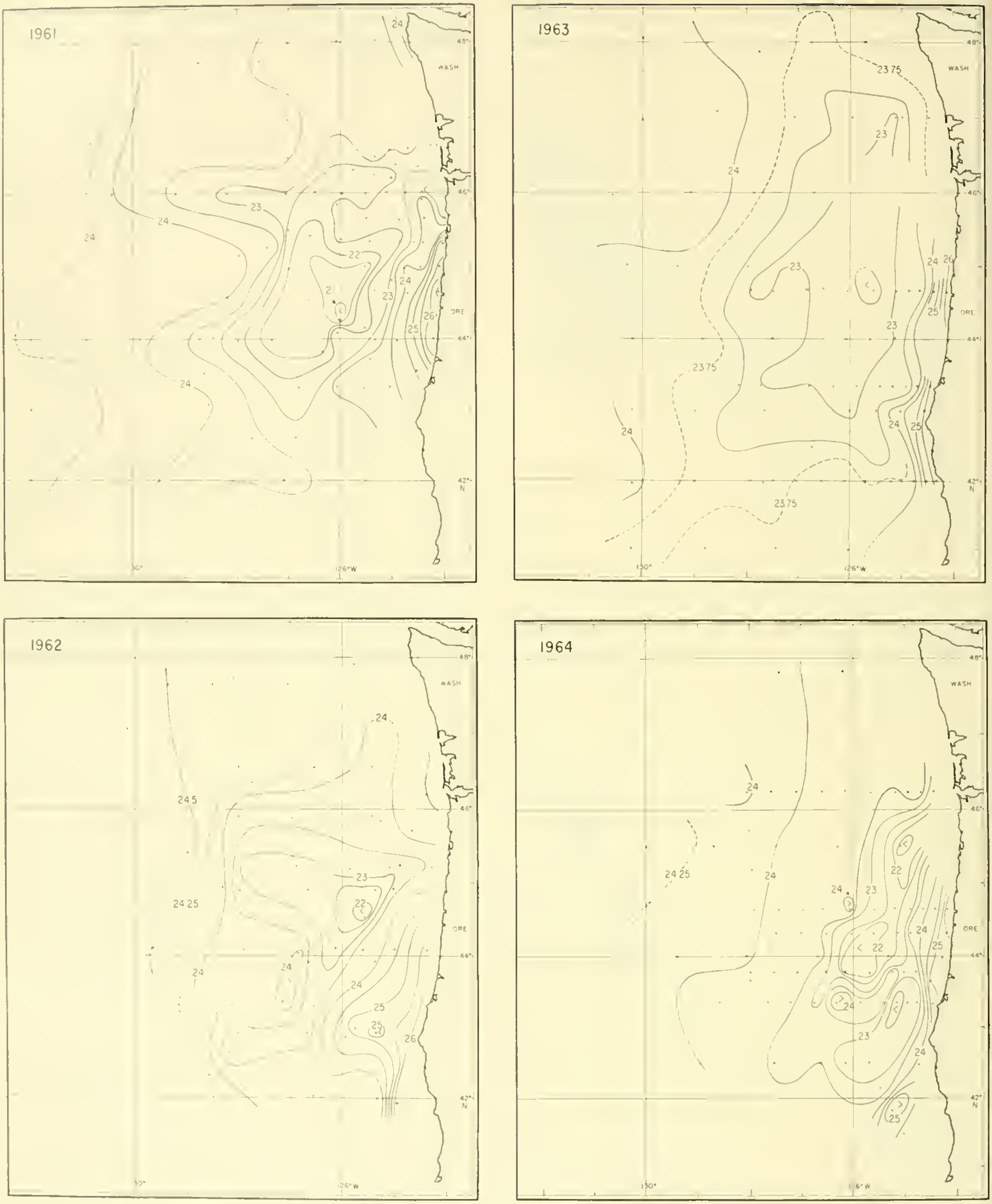
1961
1963
1962
1964
WASH
ORE
48°
46°
44°
42° N
130°
126°W
24
23
22
25
26
23.75
24.5
24.25

FIGURE 5.—July distribution of density at 10 m. depth, 1961–64. Contour interval is $0.5\sigma_t$ unit.

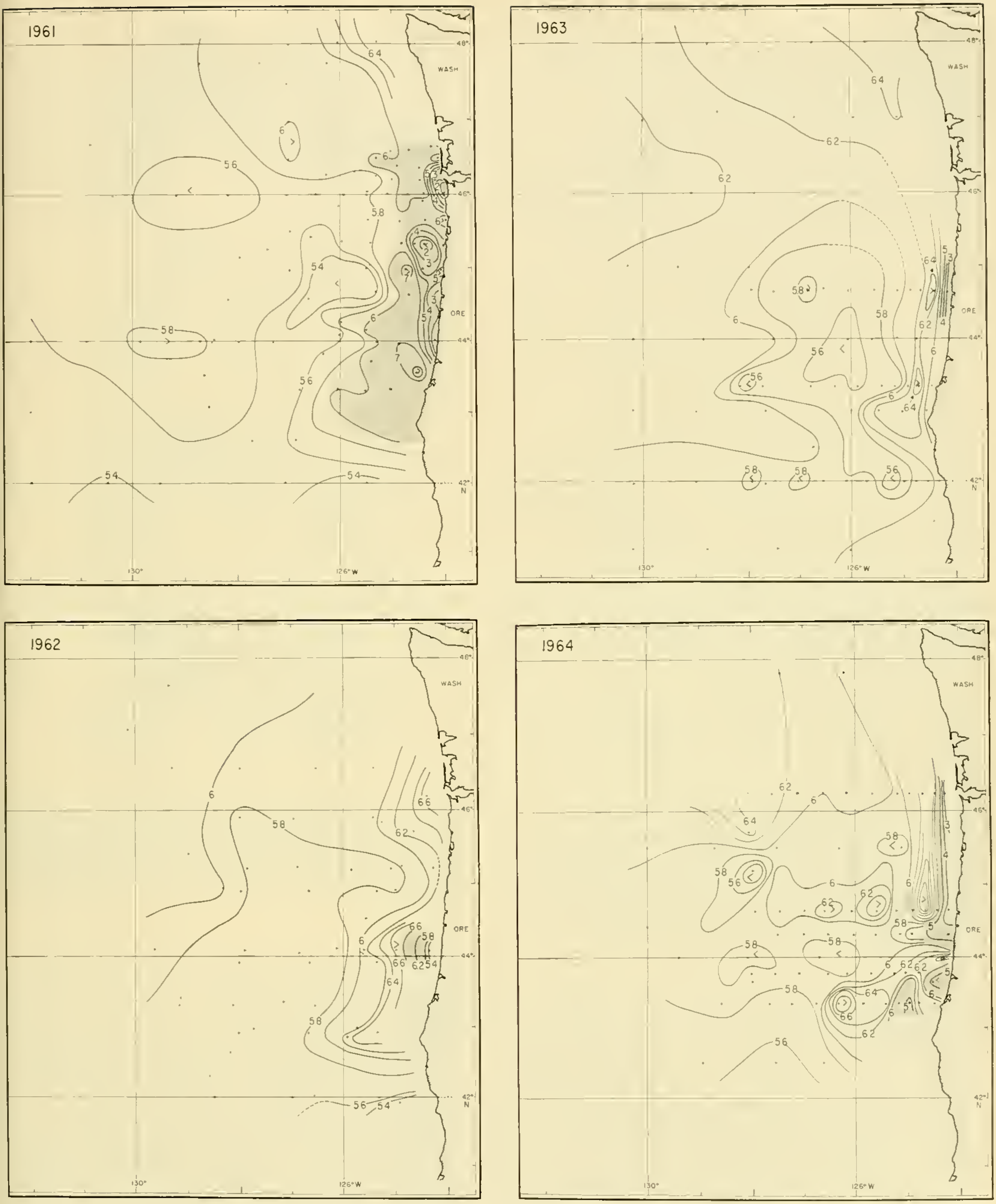
1961
1962
1963
1964
WASH
ORE
48°
46°
44°
42°
N
130°
126°W
64
62
6
58
56
54
66
7
5
4
3
2

FIGURE 6.—July distribution of oxygen concentration at 10 m. depth, 1961–64. Contour interval is 0.2 ml./l. except where shaded.

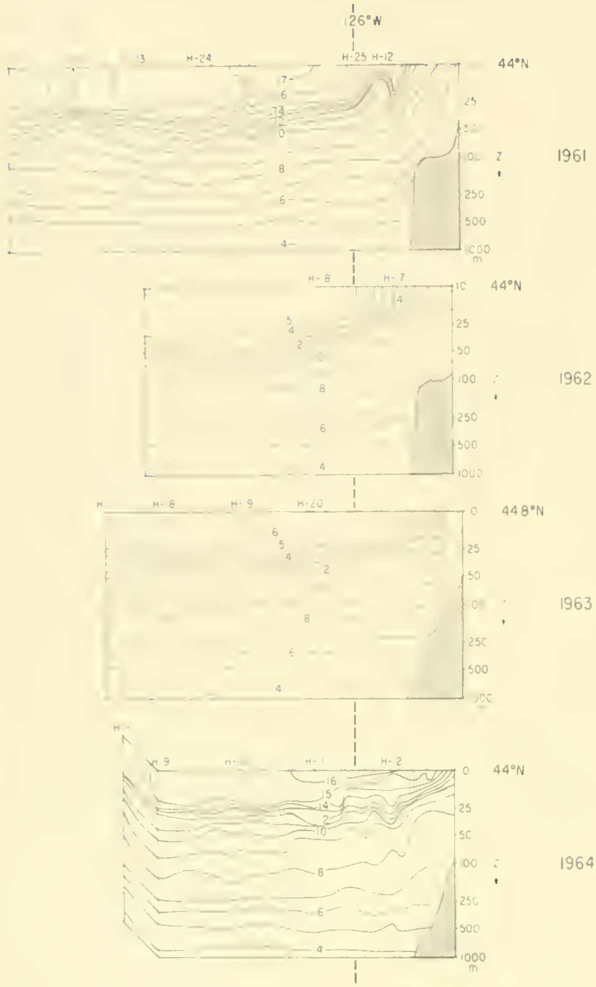

FIGURE 7.—Vertical profiles of July temperature along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 1° C. Depth scale is logarithmic. *Cobb* hydrographic stations are identified along the top of each profile. The letter Z refers to depth.

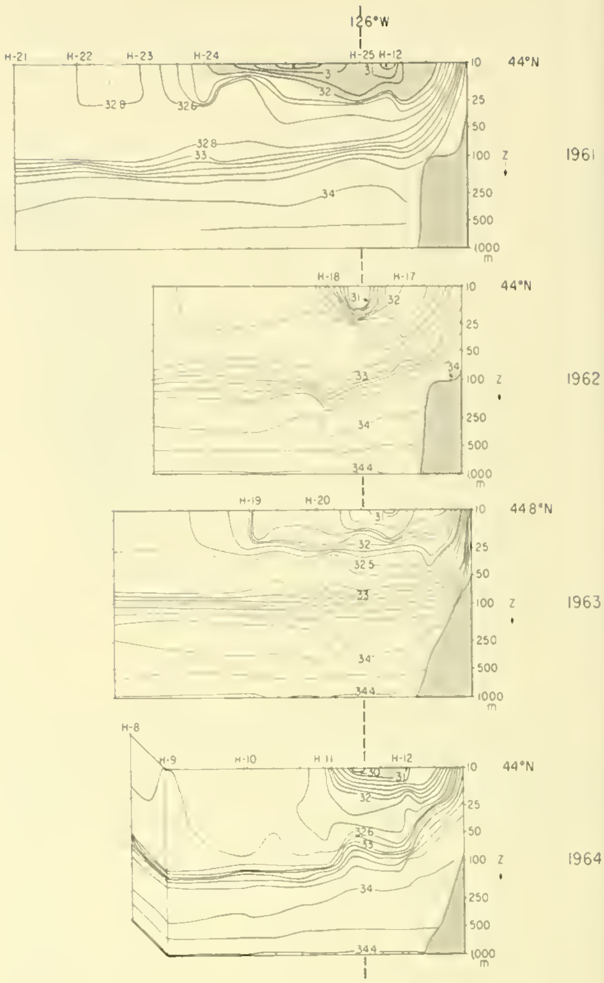

FIGURE 8.—Vertical profiles of July salinity along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 0.2°/₀₀ except where shaded. Depth scale is logarithmic.

annual discharge from all rivers along the Oregon-Washington coast (Budinger et al., 1964); probably it is the sole contributor of fresh water to the plume province in summer. For this reason, salt distribution in the surface layers of the plume province is predominantly influenced by Columbia River effluent at all times of the year. This effluent now enters the ocean at approximately the ambient offshore temperature, although its average temperature may increase in future summers as the number of Columbia River Basin impoundments increases and the June discharge pulse decreases.[1]

This discharge creates a plume of low-salinity water which in summer extends southwest from its source, in response to currents and to wind stress. Studies of the effluent by Budinger et al. (1964) indicated that estuarine mixing introduces into the open sea a mixture that consists approximately of one part river water with two parts sea water. Once a parcel of this mixture is at sea,

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[1] This temperature increase may or may not be reflected in plume temperatures in future years.

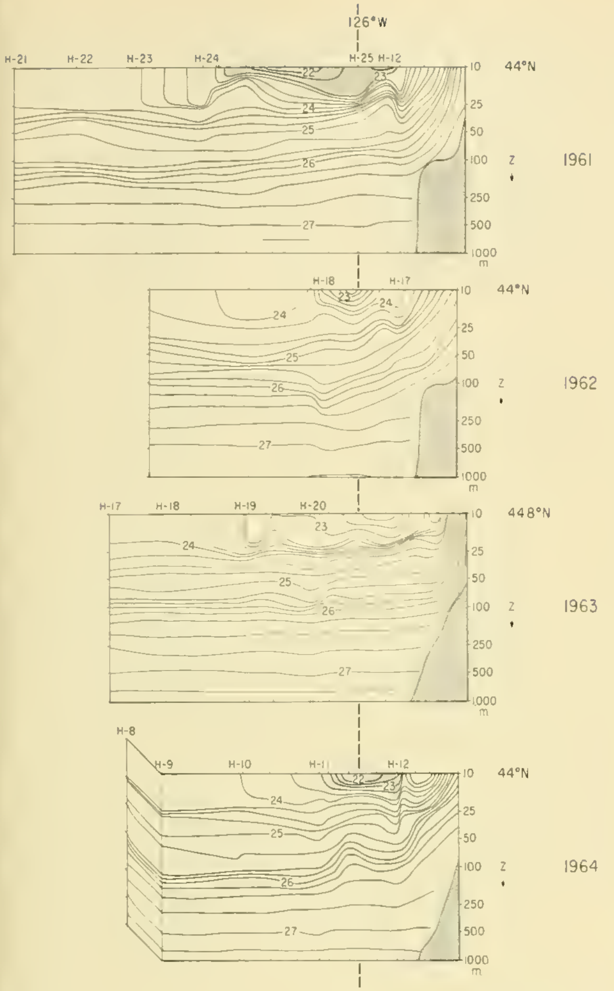

FIGURE 9.—Vertical profiles of July density along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 0.25 σ_t unit except where shaded. Depth scale is logarithmic.

entrainment and diffusion produce lateral and vertical flux of salt into the plume so that the moving parcel loses its dilute character with time and distance from its source until it is indistinguishable from water of offshore origin.

In the present treatment, the 32.2°/₀₀ isohaline is the criterion of the plume limit. This value was chosen because 32.2°/₀₀ conservatively specifies the largest value of salinity in the salinity gradient at the interface between the plume and surrounding water (figs. 4 and 8), beyond which the immediate physical influence of the plume is much diminished. The plume province thus may be defined as the portion of the area over which surface salinity is less than 32.2°/₀₀. Geographic limits of the plume, as defined by Budinger et al. (1964) for examining the fresh-water budget, were given by the location of the 32.5°/₀₀ isohaline. By this criterion, plume in summer has been detectable south of lat. 42° N. and as far as 300 nautical miles (560 km.) offshore (fig. 4), although the plume province itself does not extend so far.

The secondary halocline between plume and underlying water partly coincides with the summer thermocline (compare figs. 7 and 8 above 50 m. depth). This superposition notably increases the vertical density gradient $\partial\rho/\partial z$ over the extent of the plume province. Stability, related to the density gradient approximately by $\frac{-1}{\rho}\frac{\partial\rho}{\partial z}$ is also high; in July 1964, for example, average plume stability at 14.2×10^{-7} cm.$^{-1}$ was about 80 percent greater than average stability in the corresponding pycnocline beyond the plume.

Offshore Province.—The third subdivision, which lies seaward of the plume province, is termed the offshore province. Its character is identical with the eastern extreme of the subarctic region termed "Transitional Domain" by Dodimead et al. (1963), in that it is subarctic water with temperatures in excess of 7° C. at the top of the halocline. The offshore province may also be considered to be part of the upstream source of the California Current, since at least some of the water flows southward off the coast of California. The offshore province exhibits the vertical salinity and temperature structure characteristic of the eastern subarctic as a whole (fig. 2)—a deep, permanent halocline through which temperatures are nearly constant, and a separate, overlying summer thermocline. No strong secondary halocline is present, and salinity increases gradually and continuously with increasing depth through the layer between the summer thermocline and permanent halocline (fig. 8).

Lower Zone

Below the main halocline, coastal runoff has no direct physical influence so that only two provinces, nearshore and offshore, are distinguishable.

The nearshore lower zone is defined here as the region where the field of motion and bottom topography produce significant onshore ascent[2] of surfaces of constant density. The seaward limit of the nearshore province is not often well defined but appears to lie farther from the coast than its upper-zone analogue (figs. 7, 8, and 9). This displacement is presumed to occur because upward deflection of coastward flow occurs farther offshore with increasing depth in response to proximity of the sloping sea floor.

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[2] Ascent is here considered significant if the slope of isopleths monotonically exceeds 10^{-3} over more than two sampling locations. The term "monotonic" refers in this paper to slopes with no maxima or minima, i.e., $\partial^2/\partial z^2=0$.

Coastal upwelling in the area is largely seasonal and is caused principally by response of surface waters to the spring shift in prevailing wind direction from southwest to northwest (Lane, 1962). Because characteristics of the water in the lower-zone nearshore province are affected by this seasonal process, this province stands in contrast to that of the offshore, where seasonal changes are difficult to distinguish from nonseasonal changes (Tully, Dodimead, and Tabata, 1960).

Depth to which upwelling affects distribution of heat, salt, mass, and oxygen concentration is presumed usually to be less than about 200 m. (Sverdrup, 1938; Doe, 1955). Portions of many of the vertical sections that lie within the nearshore province, however, exhibit significant onshore ascension of isopleths of these variables at depths in excess of 250 m. (figs. 7, 8, 9, and 10).

Located beyond direct influence of bottom topography and seasonal processes, the lower-zone offshore province exhibits the horizontal uniformity of property distributions that is typical of the lower-zone subarctic. Small slopes of surfaces of constant salinity, temperature, and density indicate sluggish circulation, except where deep eddies occur. The recurrent nature of some of the closed-curve patterns that suggest eddylike motion has been noted by Budinger et al. (1964). That these patterns are recurrent implies that they do not result from internal-wave distortion of the mass field or from failure of the assumption that measurements were synoptic—possibilities suggested by Defant (1950).

Currents

The study area is largely shoreward of the region where the West-Wind Drift diverges to feed the California Current to the south and the Alaska gyre system to the north (see Dodimead et al., 1963). Previous works that included the study area (Doe, 1955; Barnes and Paquette, 1957) show weak, variable geostrophic currents that are sensitive to the influence of wind and bottom topography.

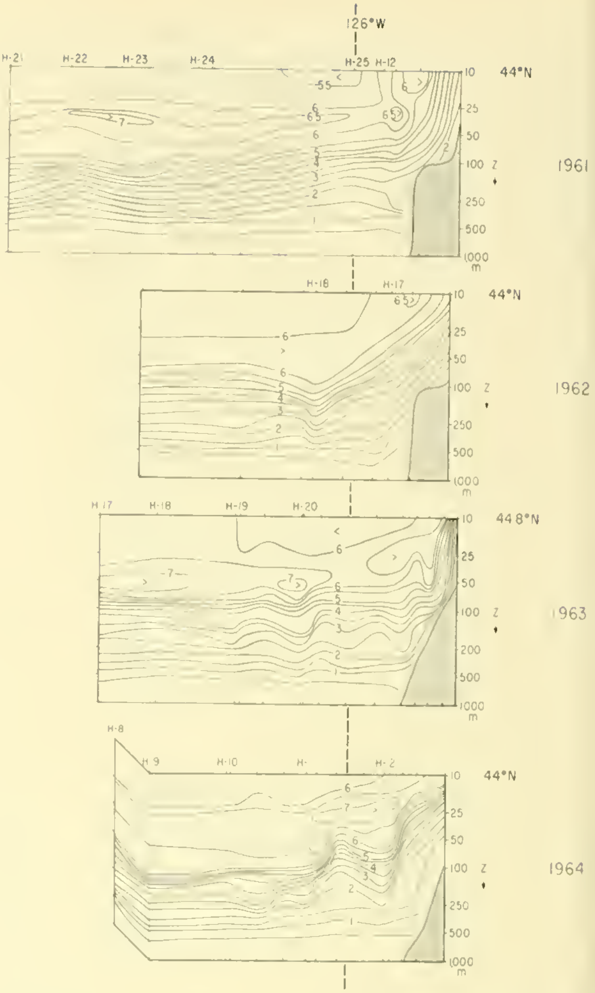

Figure 10.—Vertical profiles of July oxygen concentration along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 0.5 ml./l. Depth scale is logarithmic.

The reference level of 500 dbar. (decibars) is used in the present work; this value was selected because data were insufficient below the corresponding geometric depth. Agreement in speed and direction of geostrophic flow referred to the 500 dbar. surface with flow referred to 1,000 dbar., previously accepted as adequate for direction (Dodimead, 1961, and others), is sufficient to warrant use of the 500 dbar. level. Dodimead et al. (1963) presented flow at 500 dbar. with respect to 1,000 dbar. for summers of 1955–59. Their charts, which include the study area, indicate current speeds on the 500-dbar. surface that generally do not exceed 0.8 cm. sec.$^{-1}$; i.e., they are insignificant. Also, average flow direction referred to 1,000 dbar., and to 500 dbar. by the extension above, has been shown to agree with independent observations of ship drift over large parts of the North Pacific (Reid, 1961). No single level, however, is strictly appropriate for use as a "level of no net motion" in the subarctic. Drogue measurements in the study area (Budinger et al., 1964) indicated a weak current at 1,000 m. depth, so that slight error from this source is expected in charts of geopotential referred either to surfaces of 500 dbar. or of 1,000 dbar.

Current direction denoted by dynamic topography varies from year to year, particularly in the offshore and plume provinces (fig. 11). Geostrophic speeds, proportional to geopotential gradients, are slow and generally uniform beyond the nearshore province; values of 3 to 8 cm. sec.$^{-1}$ are typical.

Redistribution of mass due to nearshore upwelling results in a dynamic topography that consistently suggests intensified southerly flow (30–50 cm. sec.$^{-1}$) near the coast, and an eddy or loop with even greater velocities at about lat. 43° N. It is unlikely, however, that geopotential gradients reflect current velocities in nearshore areas as accurately as in the offshore and plume provinces. Time lags in the response of distribution of mass to changes in wind-driven transport probably negate the assumption of a steady state in the nearshore provinces.

The wind-induced component of flow, the Ekman transport, is superimposed on geostrophic flow in the upper layer of the sea. Ekman transport by blocks of 1° latitude, averaged zonally from longs. 130.5° W. to 124.5° W. in June and July, was calculated from the source and by the method given later in this paper. These averages demonstrate that wind-induced flow is generally to the west or southwest and that the flow—in particular its zonal component—intensifies with decreasing latitude (fig. 12). No such marked tendencies are apparent from analogous meridional averages, except that of direction.

Average current speeds computed from Ekman transport, presumed to extend to 30 m. depth, generally are lower, often by a factor of 10, than geostrophic speeds. The effect of Ekman transport on distribution of variables is probably very important, however, where Ekman transport is not parallel to geostrophic transport—in the nearshore province, parts of the offshore province, and near the plume boundaries.

Tongue Structures

Recurved, tonguelike isopleths are apparent in distributions of temperature, salinity, density, and oxygen concentration over the upper-zone waters. Along any approach to the coast from the offshore province, one thus encounters a maximum in temperature (fig. 3), minimums in salinity and density (figs. 4 and 5), and both a minimum and a maximum in oxygen concentration (fig. 6). These large-scale extremes are mainly confined to the surface layers but occur occasionally at greater depths. Each large-scale extreme, except the oxygen maximum, occurs within the area here defined as the plume province.

The salinity minimum is due simply to the presence of the low-salinity plume. In the absence of runoff, salinity at the sea surface would presumably decrease monotonically from about 33.5°/₀₀ in the upwelling areas to about 32.5°/₀₀ with increasing distance offshore.

The tonguelike ridge of higher temperatures is ascribable to two effects of the plume itself. Because the secondary halocline at the plume-sea water interface partly coincides with the thermocline, stability is augmented in this interface layer; consequently, downward heat flux through the thermocline is less than that across the unaugmented thermocline of the offshore province. Retention above the thermocline of heat gained in surface layers thus tends to be greater in the plume province than beyond. Second, this greater stability in the plume may be considered to dictate a preferred site for development of the summer thermocline at depths generally less than 20 m.[3] Wind-mixing in the offshore province, in the absence of the effect of the plume on stability, is effective to greater depths. The offshore thermocline accordingly develops at greater depths in the manner described by Tully and Giovando (1963). By this difference in mixed-layer depth (depth to the top of the summer thermocline), heat gained in the surface layer is constrained to a smaller volume in the plume than offshore, and hence the plume province has higher summer temperatures. The shoreward decrease of temperature in the nearshore province results simply from upwelling of cold water.

A measure of the extent to which the plume

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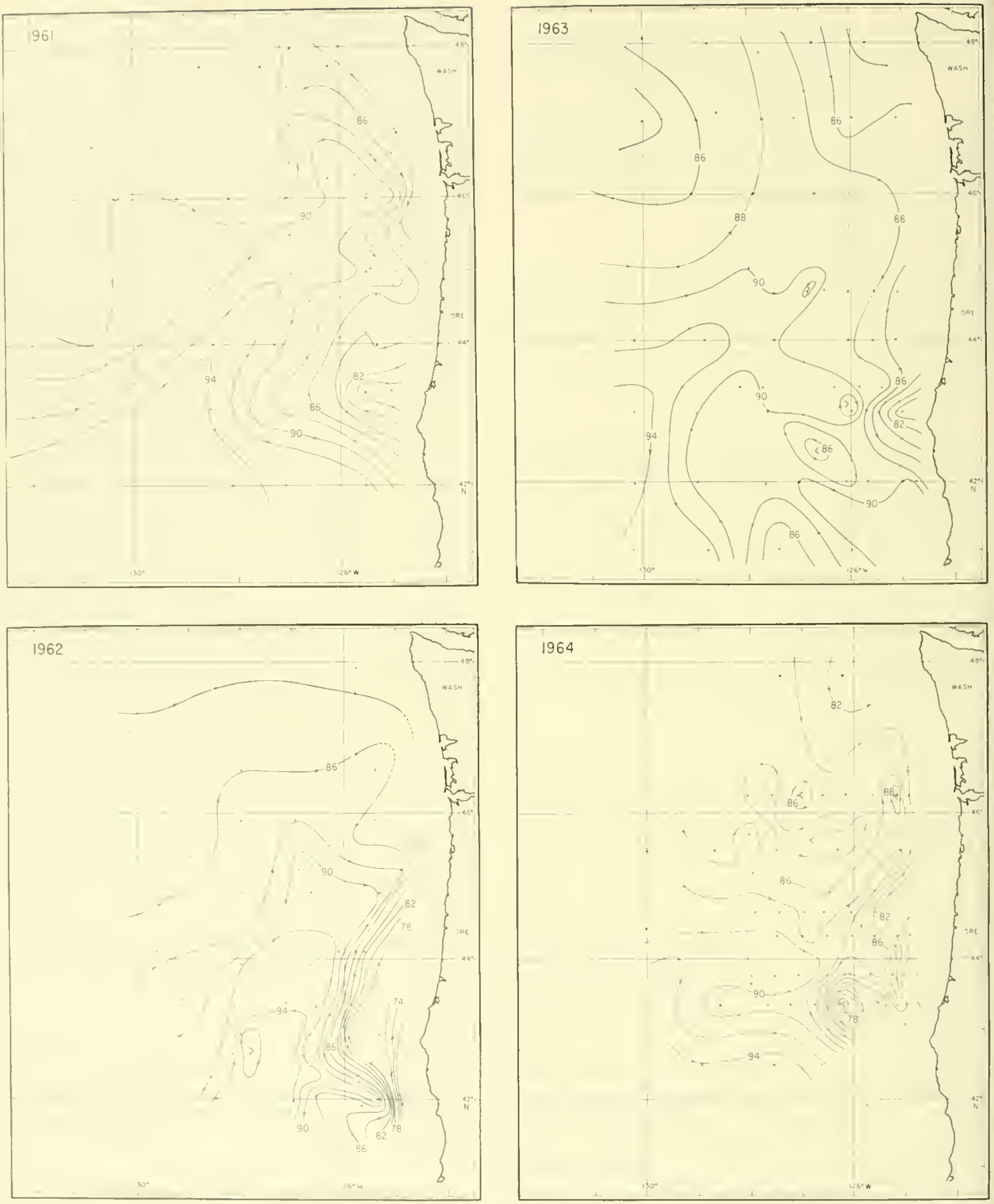
[3] With the partial exception of July 1963, the offshore limit of the plume province is in fact approximated by the 20-m. isopleth of thermal mixed layer depth (fig. 13).


1961
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88
86
90
90
86
82
94
86
90
86
1962
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82
78
94
74
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90
82
78
86
1964
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78
94

Figure 11.—Geopotential topography of the July sea surface relative to 500 dbar., 1961–64. Contour interval is 2 dynamic cm.

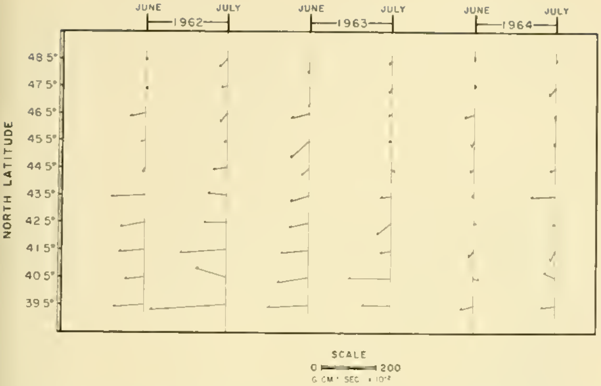


FIGURE 12.—Wind-driven (Ekman) transport vectors by 1° increments of latitude, averaged between longs. 124° W. and 130° W. Length of vectors gives transport in g. cm.$^{-1}$ sec.$^{-1}$ according to the scale below figure.

influences heat constraint, and therefore temperature distribution, is provided by figure 14. As implied by figure 2, the permanent halocline is the lower limit of winter mixing; consequently temperature near the top of the permanent halocline is nearly identical to that of the mixed layer in the previous winter (Dodimead et al., 1963). Hence the July difference between temperature at the sea surface and the temperature where salinity equals 33°/₀₀, located within the halocline, is a measure of mixed-layer temperature change, $\Delta\theta$, from the previous winter. The area of greater temperature change substantially corresponds to the plume province as defined by surface salinity distributions (fig. 4).

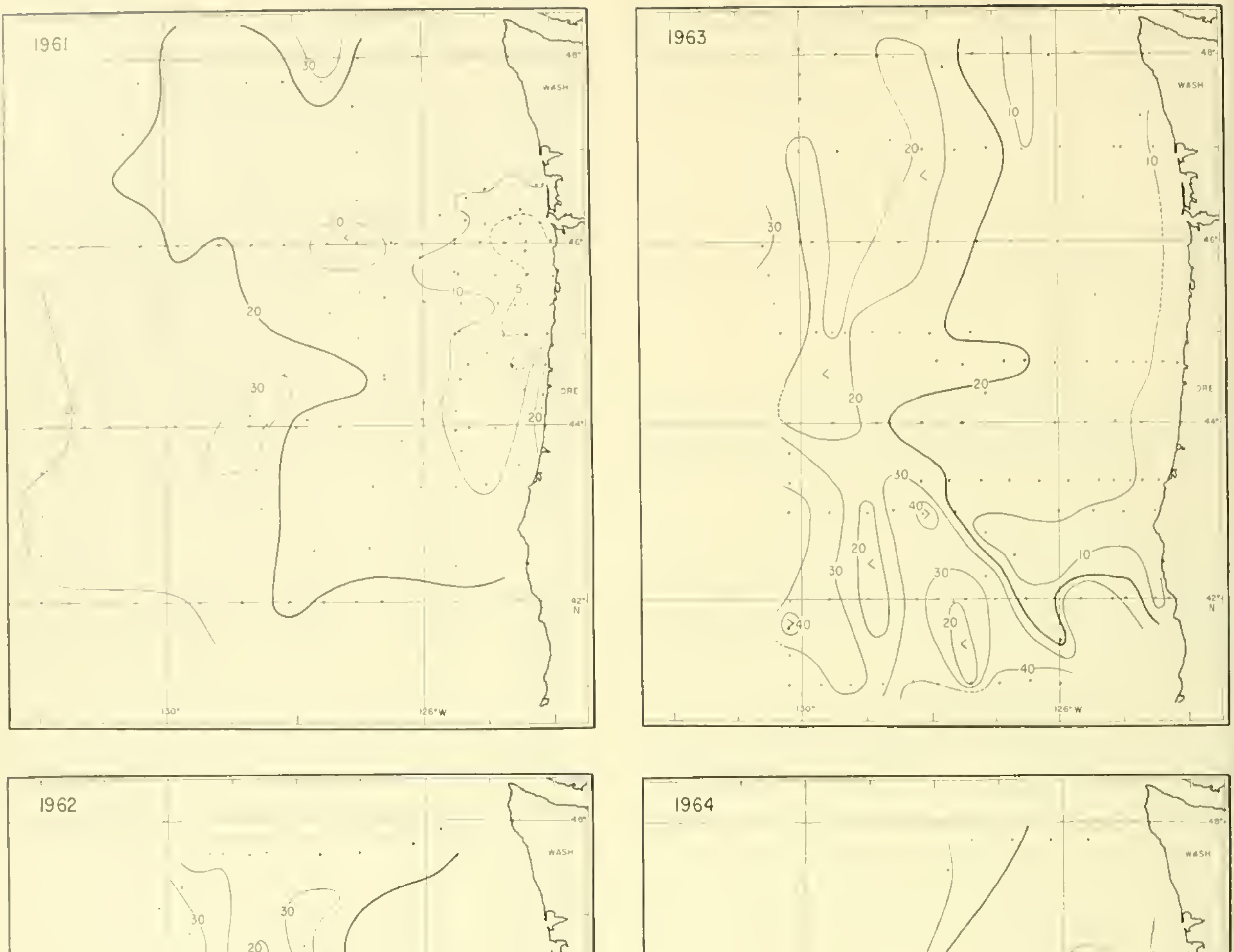
The summer tongue of lower density in the plume province (fig. 5) is produced by the coincidence of tongues of low salinity and high temperature described above.

Distribution of oxygen concentration in the near-surface layers is more complicated than that of the preceding variables. Shoreward of the minimum (5.4–6.5 ml./l.) in the plume province are a maximum (6.6–8.0 ml./l.) in the seaward portion of the nearshore province and a minimum (2.0–5.0 ml./l.) nearest the coast. These extremes combine to produce the trough-and-ridge oxygen distribution that was characteristic of the area in each summer in 1961–64, except the last (fig. 6).

The oxygen minimum in the plume is the result of the larger influence of reduced oxygen solubility at higher temperatures over the opposite influence of higher oxygen solubility at reduced salinities. Since the degree to which waters of the surface layer are saturated with oxygen is the same in the offshore as in the plume province (about 104 percent), this variation is not attributable to differences in biological processes.

In the horizontal distribution of oxygen, the presence of both the minimum and maximum concentrations in the surface layer of the nearshore province is the product of one or both of two effects of upwelling. Upwelling transports nutrient-rich water that is undersaturated with oxygen into the photic zone, where algal photosynthesis increases the oxygen concentration sufficiently to produce supersaturation. If the transfer of oxygen from the air to the sea proceeds faster than the transfer of heat, supersaturation can result independently from this purely physical process. The oxygen minimum along the coastal portion of the nearshore province may thus represent that part of the upwelling system where the residence time of low-oxygen water in the surface layer has been too short to exhibit effects of local oxygen gain by photosynthesis and atmospheric exchange. Conversely, the maximum in the outer part of the nearshore province represents the area where one or both processes have been operating for sufficient time to effect supersaturation. Large standing stocks of phytoplankton, indicated by higher chlorophyll concentrations (Owen, 1967b) and larger rates of carbon assimilation nearshore (Anderson, 1963), support the hypothesis of greater oxygen production by photosynthesis in the fertile nearshore province than beyond. That local processes of oxygen gain are effective in this province is evident from the decreased slopes of near-surface oxygen isopleths (fig. 10) relative to isohaline slopes (fig. 8). In the absence of local oxygen gain, these slopes would be identical.

The nearshore maximum in the horizontal distribution of oxygen may also be ascribed to a more direct effect of upwelling. Seaward of the nearshore province, a maximum value (5–7 ml./l.) in the vertical distribution of oxygen concentration occurs in summer at depths of 30 to 70 m. (fig. 10). This maximum is not confined to the present area, but is present over large parts of the North Pacific, where it has been ascribed to summer loss of oxygen above the layer in which the maximum occurs (Reid, 1962; Pytkowicz, 1964). Summer upwelling in the nearshore province would displace the layer of this oxygen maximum upward to form the horizontal maximum in the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30

FIGURE 13.—Depth of the upper mixed layer in July 1961–64. Contour interval is 10 m.

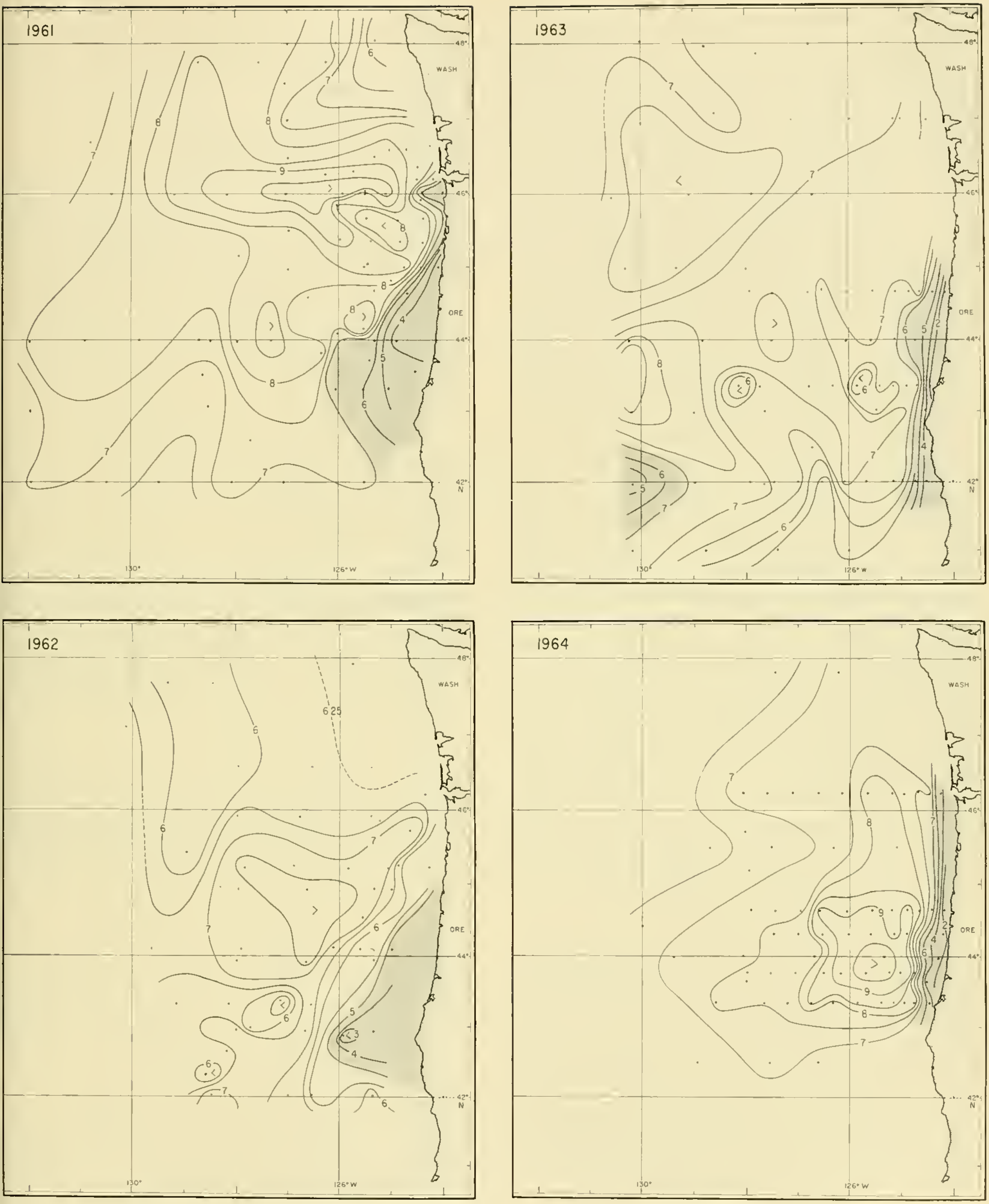
1961
1963
1962
1964
WASH
ORE
48°
46°
44°
42° N
130°
126° W
6.25

Figure 14.—Difference between surface-layer temperature and temperature at the depth where salinity equals 33‰, 1961–64. Contour interval is 0.5° C.

near-surface layer (fig. 6). Stefánsson and Richards (1964, p. 374), on the other hand, have suggested that offshore movement and subsequent sinking (along isentropic surfaces) of upwelled water which has gained oxygen from photosynthesis would "largely contribute to the formation of the (offshore vertical) maximum." If so, then the near-surface horizontal maximum would presumably result. It seems unlikely, however, that this process alone could generate the vertical maximum that occurs widely over the North Pacific; definitive measurements—e.g., apparent phosphate uptake (APU) in the layer of the offshore oxygen maximum—are not yet available to indicate whether the vertical oxygen maximum of the plume and offshore provinces is derived from the nearshore, near-surface horizontal maximum, or, conversely, whether it produces the nearshore maximum by upward displacement.

Oxygen distribution in the near-surface layer apparently was atypical in the summer of 1964 (fig. 6). The basic pattern described above was altered in the plume by the presence of well-developed pockets of high concentrations of oxygen. Production of some pockets by phytoplankton photosynthesis is indicated from their high degree of supersaturation (106–110 percent) and from generally large concentrations of chlorophyll *a* in the plume and offshore province in 1964. High-oxygen pockets were associated with low temperatures (13–14.5° C. at 10 m.). Heterogeneity of their mode of generation is indicated, however, by the large corresponding range of salinity (30.5–32‰ at 10 m.), and one pocket, centered at lat. 43.3° N. and long. 126.2° W., clearly was produced as part of a dome formed by the motion of a cyclonic eddy (fig. 11).

Tonguelike patterns occur occasionally at greater depths (100 m. or more) but not with sufficient frequency to be considered recurrent or characteristic. It is difficult to see how these tongues could arise from the same mechanisms that produce near-surface tongues. Because of the nearly uniform temperature-salinity relation beneath the near-surface layer, the tongues at the greater depths appear to be produced by the distribution of mass associated with geostrophic flow.

ANNUAL VARIATIONS

Differences from year to year in extent and character of provinces are generated by changes in the dominant processes. The basic patterns discussed in the previous section are not obscured, however, but are altered only in degree. Effects of these differences upon heating in the surface layers are discernible.

Extent and Character of Provinces

The state of development of the nearshore province is determined principally by the intensity and duration of upwelling, which in turn depends upon the nature of the coastal wind field and upon local bathymetry. Because bathymetry is fixed, between-year differences in the extent of the nearshore province should be assignable to differences between years in the June and July wind fields. A means of assessing the effect of wind field on upwelling is provided by estimation of average zonal components of Ekman transport across the near-coast meridian 124.5° W. Wind data for the study area in June and July 1962–64 were obtained from monthly summaries of marine weather observations for the Pacific Ocean prepared by the Tuna Resources Laboratory, Bureau of Commercial Fisheries, La Jolla, Calif., in the form of average zonal and meridional components of wind velocity by 1° squares. Average wind stress, $\overline{\tau}$ (g. cm.$^{-1}$ sec.$^{-2}$), was computed from average wind velocity, $\overline{U}$ (assumed to have been measured at 10 m. above sea surface), by the basic equation

$$\overline{\tau}=\rho C_D U^2$$

where air density, ρ, is taken to be constant at 1.2×10^{-3} g. cm.$^{-3}$ and $C_D=(1+0.07U) \times 10^{-3}$ (Deacon and Webb, 1962, p. 61). The computing equation, with constants adjusted for the use of U in knots, is

$$\overline{\tau}=0.318\overline{U}^2(1+0.036\overline{U}) \times 10^{-2} \qquad (1)$$

Because instantaneous values of wind velocity were not available from the summary described above, equation (1) was entered with averaged values of wind speed $(\overline{U})$. Because $(\overline{U})^2<\overline{U^2}$, values of $\overline{\tau}$ used here underestimate the true averages of wind stress.

Ekman transport, which is assumed not to extend beyond the bottom of the pycnocline produced by the thermocline and plume halocline, is given by integration of equations of motion with appropriate boundary conditions:

$$M_x=\tau_y/f$$

$$M_y=\tau_x/f$$

where f, the Coriolis parameter, is evaluated for present purposes at lat. 45° N. The zonal component was computed for each degree of latitude from 39.5° N. to 48.5° N. along long. 124.5° W., and then averaged to give mean zonal transport in g. cm.$^{-1}$ sec.$^{-1}$ for June and July 1962–64. The results indicated that the intensity of upwelling was highest in June and July of 1962, when the offshore transport across 124.5° W. was largest, and lowest in June and July of 1964, when offshore transport was least (table 1). Wind data are not available for June and July of 1961.

TABLE 1.—*Average zonal component of Ekman transport, M_x(g. cm.$^{-1}$ sec.$^{-1}$$\times 10^{-3}$), westward across long. 124.5° W. from lat. 39.5° N. to 48.5° N., for June and July 1962–64*

Year	June	July	Average
1962	6.77	8.75	7.76
1963	3.67	5.89	4.78
1964	3.34	0.72	2.03
Average	4.59	5.12	4.86

Correspondingly, oceanographic evidence indicates greater upwelling in 1962 than in 1963 or 1964. Local heating of upwelled water, as pointed out previously, precludes use of near-surface temperature and density for assessment of upwelling. Salinity, however, is little changed by processes other than diffusion and upwelling, and thus provides the best available estimator of upwelling effects. The extent of the nearshore province and, therefore, July development of upwelling may be compared between years by noting the distance from the coast at which the 32.5‰ isohaline is first encountered at the sea surface. The mean distance of this isohaline from the coast was about 50 nautical miles (90 km.) in 1962, but less than 20 nautical miles (35 km.) in 1961, 1963, and 1964. These distances indicate a significant seaward extension of the nearshore province in 1962. The rather precise nearshore coincidence of the 32.5‰ isohalines in 1961, 1963, and 1964 suggests close similarity of upwelling in these years and further heightens the contrast of 1962 conditions. Similar checks on the near-surface distributions of other less conservative properties (temperature, density, oxygen concentration) confirm qualitatively that upwelling effects were markedly pronounced in July 1962. Secondary effects of differences were not apparent; extremes were observed in the plume in years when intensity of upwelling in the nearshore province was similar.

Closer correspondence of June transport than of July transport to the July distributions of properties suggests an appreciable time lag in the response of the nearshore province to changes in wind field. Prediction of upwelling conditions by computations from coastal wind field of the previous month may thus be possible.

The extent and character of the plume province have exhibited the greatest variation from year to year. Differences in size and intensity of the plume itself, shown by comparison of values and gradients in near-surface salinity distributions (fig. 4), suggest large year-to-year differences in the balance of processes that determine plume distribution—volume of discharge from land, diffusion, and advection.[4] For the period 1961–64, summer conditions in 1963 and 1964 displayed maximum contrast. The plume in July 1963 showed the weakest development; though the area was large the salinity was high and the horizontal gradients were exceedingly small. In spite of less than normal June discharge of fresh water into the province, the depth of the secondary halocline in the plume was not notably less in 1963 than in other years (fig. 8). The small horizontal gradients and large values of salinity in the upper layers of the plume thus show that lateral diffusion and zonal advection were relatively more effective than meridional advection in distributing plume water. Indeed, the smaller zonal gradients of dynamic height of July 1963 (fig. 11) indicate diminished southward transport by the geostrophic component of motion, whereas wind-velocity fields in June and July 1963 indicate large offshore displacements by the Ekman component of motion (fig. 12), particularly to the south of lat. 44° N.

The July 1964 plume, at the other extreme, was highly constrained and was characterized by low salinities (< 27‰ at one offshore station) and by large horizontal gradients of salinity. The meridional constraint of the 1964 plume, together with the observation that the discharge in June 1964 from the Columbia River was largest of the years considered (table 2, last column), indicates dominance of meridional advection over zonal advection and diffusion in plume dispersion. In contrast to flow conditions in 1963, southward transport by the geostrophic component of motion in July 1964 is indicated to be larger (fig. 11) and to predominate over transport by the much diminished Ekman component of June and July 1964 (fig. 12).

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[4] The effects of time-dependent hydraulic mixing near fresh-water sources, which presumably would determine the characteristics of water in the plume province, are here considered to have been "averaged out" in the time required for water to transit the nearshore province and enter the plume province.

The plumes of 1962 and 1963 would be expected to be similar on the basis of the similarity of June-July wind-induced transports (fig. 12) and of June discharge rates from the Columbia River. They differed markedly, however, in salinity. Although the 1962 plume was nearly as broad as that of 1963, it displayed larger gradients and smaller values of salinity; these differences imply reduced importance of diffusion processes during 1962. Because wind effects were about equal in the 2 years, differences in the geostrophic component of flow must have caused this difference in the relative importance of diffusion, and (together with variation in river discharge volume) the differences in salinity characteristics of the plume. Comparison of dynamic height patterns of the 2 years (fig. 11) reveals two significant differences in the nature of geostrophic flow: greater current speeds and a pronounced northward component in the outer plume province and offshore province in 1962. The apparent reduction of diffusion effects relative to advective effects in 1962 was accomplished by faster geostrophic transport of the plume. Further, the breadth of the 1962 plume and the lateral disposition of pockets of less saline water could have been the consequence of transport of the plume from southwest to northeast, indicated by geostrophic flow in the offshore part of the study area.

Geostrophic flow in 1961 was similar to that of 1962 in current speeds and in the presence of the offshore northward component; probably the plumes of the two years were produced by the same balance of forces. The principal difference between the two plumes was in salinity—the 1961 plume was less saline than that of 1962. This difference appears to have resulted from high runoff in 1961: average discharge rate of the Columbia River for June 1961 was about 1.7 x 10^4 m.^{3} sec.$^{-1}$ or 1.5 times greater than the discharge for June 1962 (estimated from Budinger et al., 1964, fig. 34, p. 51).

Differences between years in near-surface salinity of the offshore province were insignificant.

Heating

The general effect of the fresh-water plume on temperature was described above. Briefly, heat is constrained to a smaller volume in the plume than beyond so that, by July, plume temperatures exceed offshore temperatures. Because the degree of plume development varied widely from summer to summer during 1961–64, one may reasonably expect to see variations among the respective temperature distributions.

Temperature of the mixed layer in July at any location in the study area may be considered to be the net expression of the following factors: temperature at the start of the heating season (about March); heat gain, principally across the sea surface, between March and July; heat loss by advection and diffusion; and depth over which heat changes are distributed (thickness of the mixed layer and thermocline). If it is assumed for present purposes that advective heat change is important only in the nearshore regime (as upwelling), and that the meridional gradient of heat-exchange across the sea surface is constant while the zonal gradient is zero over the study area, then one must only consider variation of initial temperature, lateral and vertical diffusion, and free-mixing depth to explain the mixed-layer temperature patterns of figure 3.

July temperature near the top of the permanent

TABLE 2.—*Maximum temperature changes and salinity gradients in the plume province and average discharge rates of the Columbia River, 1961–64*

[Ranks are provided to facilitate comparisons]

Year	Mid-plume temperature change from previous winter to July		Average vertical salinity gradient at plume boundary, lat. 44° N. in July		Average horizontal salinity gradient normal to plume boundary in July		Average of the Columbia River discharge rate in June	
	$\Delta\Theta$ (°C.)	*Rank*	$\partial S/\partial z$ (°/₀₀ m.$^{-1}$)	*Rank*	$\partial S/\partial n$ (°/₀₀ km.$^{-1}$)	*Rank*	$\partial V/\partial t$ (10^3 m.^{3} sec.$^{-1}$)	*Rank*
1961	8.5	2	0.6	2	0.041	2	17.0	2
1962	7.5	3	.4	3	.022	3	11.9	3
1963	7.0	4	.2	4	.006	4	11.7	4
1964	9.5	1	1.0	1	.092	1	17.5	1

halocline, as noted above, is a measure of the minimum mixed-layer temperature of the previous winter. By definition, minimum temperature occurs at the beginning of the heating season. Seaward of upwelling influence, distribution of July temperature at 100 m. thus approximates the initial field of temperature. Temperature variation at this depth did not generally exceed 1° C. over the plume and offshore provinces, either spatially or from year to year (Owen, 1967b). Compared with spatial and temporal temperature changes in the near-surface layer, this variation was small enough to permit the assumption that none of the variation of July mixed-layer temperature was due to initial temperature differences.

Two sources of variation remain: thermal diffusion and mixing depth. Both may be expected to be substantially affected by salinity gradients at plume-sea interfaces, so that their effects on temperature distribution may be treated collectively as the "plume effect." It is this influence to which the recurrent ridge of higher temperatures was ascribed in the previous section.

On this basis, the validity of the proposed plume effect can be examined by comparing the pattern of plume disposition with the pattern of near-surface temperature change from the respective winters. Average values of salinity gradients normal to the plume edges were estimated from figure 4 (horizontal gradient estimates) and figure 8 (vertical gradient estimates along lat. 44° N.) and entered with values of maximum within-plume temperature change in table 2. The association of larger temperature change within the plume with large plume-edge gradients is clear from this table as well as from the figures themselves.

To examine the plume effect further, mixed-layer temperature change, $\Delta\theta$, was plotted as a function of surface salinity for each July of the 4 years on the basis that surface salinity inversely represents the degree of "presence" of the plume and hence the magnitude of its interface gradients. Sets of paired data from each hydrographic station for each year were subjected to Spearman's rank-difference correlation test (Tate and Clelland, 1957); testing showed significant inverse relation at levels of $p<0.001$ for 1961, $p<0.001$ for 1962, $0.1<p<0.2$ for 1963, and $p\ll0.001$ for 1964. Differences between these levels of significance appear to depend on the degree of plume development and salinity gradients.

Validity of the assumed sea surface heat-exchange field must remain an open question. It is difficult, however, to see how the particular field of heat exchange could arise to produce the closed curves of $\Delta\theta$ in the plume regime in the absence of oceanographic mechanisms discussed previously. The lack of advective heat change in the plume and offshore provinces is certain to be an approximation: ridgelike dynamic topography indicates possible advective transport of warmer offshore waters of more southern origin in 1961 and 1962. That this approximation is sufficiently good for showing the plume effect, however, is indicated by the differential heating in the plume in 1964, in spite of a flow pattern that suggests advective transport of colder water from the northwest. Advective effects thus appear to be masked by local change.

SUMMARY OF OCEANIC PROCESSES AND VARIATIONS OFF OREGON AND WASHINGTON

The region studied off the coast of Oregon and Washington is divisible in summer into three oceanographic provinces above and two provinces below the main halocline. This division is based on discontinuities in the distributions of variables that denote discontinuities in the influence of physical mechanisms, so that the oceanographic processes may be considered similar within and dissimilar between provinces. These processes—upwelling in the nearshore province, modification by land runoff in the plume province, and net dilution of surface layers in the offshore province—produce recurrent distributions of heat, salt, mass and, together with biological processes, oxygen.

Annual variations in the distribution of variables are attributable to changes in wind field, in fresh-water discharge from the land, and in advection. The variations are not sufficiently large, however, to obscure the basic patterns generated by dominant processes.

The balance of processes off Oregon and Washington is atypical in one respect. Whereas advection strongly influences recurrent patterns of near-surface distributions in oceanic regions lacking large fresh-water sources, its role in the study area is limited to disposition of land runoff. The low-salinity plume itself establishes the conditions for differences in local processes that generate the recurrent distribution patterns described here.

RELATION OF PHYSICAL PROCESSES TO THE ALBACORE FISHERY

It is particularly desirable to attempt to correlate the environmental conditions encountered each year by albacore when they first enter the region off Oregon and Washington with the subsequent distribution and numbers of fish available to the fishery. Suggested relations of environmental mechanisms to potential success of the fishery (that rarely extends seaward of the plume province) may then be tested in a preliminary fashion.

It appeared early in the analysis that the Oregon-Washington fishery for albacore might owe its degree of success to effects of the plume rather than despite them—i.e., that the limit of the area which contains commercial quantities of albacore might be locally extended to the north by these effects. Larger catches and catch rates of the *John N. Cobb* at and within the lateral limits of the plume than beyond it support the proposal that numbers of available albacore generally are higher in the plume than beyond (table 3, fig. 15).

TABLE 3.—*Summary of albacore trolling in July by M/V "John N. Cobb" off the Oregon-Washington coast, 1961–64*

[Effort is summed from day of first catch]

Year	Area of catch				Ratio of catch/effort (within/beyond)	
	Within plume [1]		Beyond plume [2]			
	Effort	Catch/effort	Effort	Catch/effort	Value	Rank
	Line-hours	*No./100 line-hours*	*Line-hours*	*No./100 line-hours*		
1961	602	7.5	647	1.4	5.4	3
1962	705	33.3	<10	(3)	(2)	(2)
1963	568	24.8	234	0.4	62.0	1
1964	202	16.3	183	22.4	0.7	4

[1] Where $S<32.2$‰.

[2] Where $S>32.2$‰.

[3] Catch per unit of effort was not measured because effort was insufficient outside the plume province after the day of first catch within it. On the basis of 316 line-hours expended outside the plume before the day of first catch, however, it can be said that the availability of albacore was far greater within the plume than outside it.

One physical mechanism to which these concentration effects may be related is the greater retention of heat within the surface layer of the plume province. This retention, coupled with wind-induced upwelling in the nearshore provinces, produces the temperature ridge discussed earlier. By extension of previous examples of albacore-temperature relation (e.g. Alverson, 1961; Johnson, 1962) we may assume that, at any instant of the fishery period, albacore will tend to concentrate in the region where temperature is most nearly optimal and will be absent from regions where surface-layer temperatures are less than 13° C. From smoothed plots of albacore catch frequency as a function of sea surface temperature for the fishery off California (Glenn Flittner, personal communication), 18° C. appears to be the optimal temperature. This temperature is seldom exceeded in the study area in July and is only barely exceeded in August and September. Consequently, after the albacore had moved into the region, we would expect the largest concentrations of fish to develop in the areas with the highest water temperatures or in the plume province rather than in the colder waters of the nearshore or offshore provinces.

Furthermore, in the absence of other environmental effects, relatively more albacore would be expected to be in the plume than outside it in years of greater temperature increase, when the plume is most sharply defined; then catch rates should be higher in the plume province than offshore. This expectation was not upheld, however: comparison of temperature change and plume intensity with average catch rates of fishing by the *John N. Cobb* within the plume province (table 3) and concurrent July–August averages of catch per unit of effort for the commercial fishery in the study area (fig. 16) showed that greater than average numbers of albacore were available in 1962 and 1963, when July temperatures were lower (fig. 3) and temperature changes (table 2, fig. 14) were smaller, than in 1961 and 1964. Furthermore, the ratio of catch rate within the plume to that beyond the plume (table 3) was largest in 1963. These differences in catch rates indicate that albacore concentrated in the plume to a greater degree when the difference in July temperatures in the plume and offshore provinces was least (fig. 3).

These results indicate that at least one variable other than temperature affects the distribution of albacore over the provinces. One factor is variation in catch rate and its relation to abundance of available albacore. If the catch rate for each province adequately represents the number of available albacore, then the ratio of catch rate within the plume to that beyond is free of influence by total abundance of albacore. The agreement of catch rates for exploratory fishing in the plume each year with respective July and August

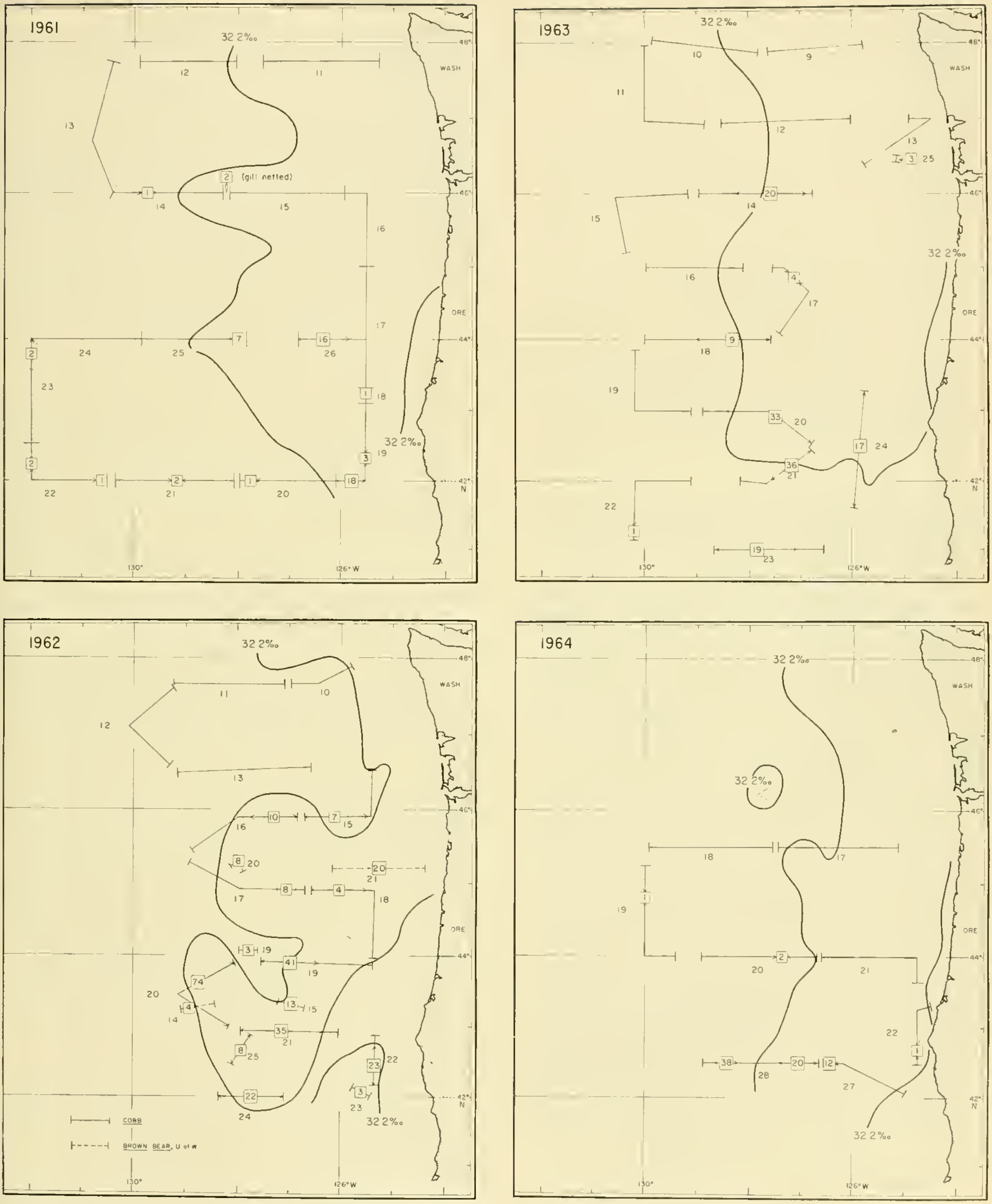
1961
32.2‰
WASH
ORE
48°
46°
44°
42° N
130°
126° W
(gill netted)
1963
1962
1964
COBB
BROWN BEAR, U of W

FIGURE 15.—Albacore catches (boxed numerals) by M/V *John N. Cobb* in July 1961–64, with corresponding lateral plume limits (32.2 °/₀₀ isohaline). July dates are given below or beside track line segments.

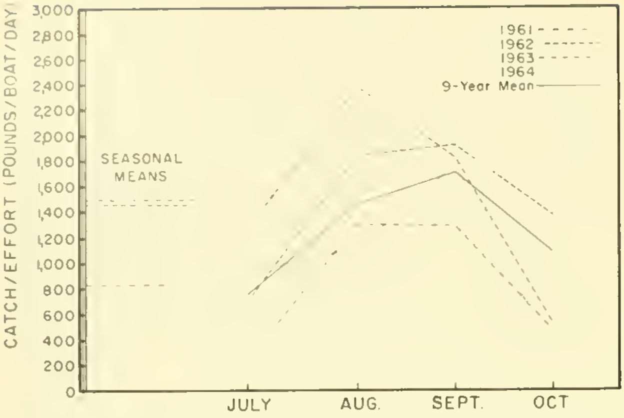

FIGURE 16.—Monthly averages of catch per unit of effort (pounds of albacore per boat-day of fishing) for the area north of lat. 40° N., east of long. 130° W. Data from Ayers and Meehan (1963) and James Meehan (personal communication) for effort exceeding 5 days per 1° square in the month.

catch rates for the commercial fishery in the plume province, although imperfect, indicates that the catch rates for exploratory fishing are adequate for use as ratios in the following discussion.

Still another factor is salinity. Nowhere over their known distribution do migrating albacore encounter a greater range of salinity than in the region off Oregon and Washington. Albacore thus may respond not only to temperature variation, as described above, but also to variation of salinity in the plume—for example through its effect upon balance of osmotic pressure. This balance, the difference between the organism's internal and environmental osmotic pressure (both referred to pure water at 0° C.), was studied by Sakamoto (1962) as a mechanism for determining movements of pelagic fishes and was applied to the Japanese fishery for yellowtail (*Seriola quinqueradiata*, Temminck and Schlegel).

Albacore, like other teleosts, must maintain their internal osmotic pressure at a nearly constant level so that pressure balance is a function only of environmental osmotic pressure. Rewritten from equations of Thompson (1932) and of Lyman and Fleming (1940) in terms of salinity and temperature, the unified expression for osmotic pressure of sea water, π, is (in millibars)

$$\pi(S\text{‰}, \theta) = (130.067\ S\text{‰} + 5.051)\ (0.018\ \theta + 5.051).$$

Salinity variation clearly dominates variation of environmental osmotic pressure in the surface layer, and hence the osmotic pressure balance experienced by albacore.

If albacore move so as to maintain a constant balance of osmotic pressure, the response of albacore to more favorable temperatures in the plume would be diminished or even canceled by their negative response to low salinity. Support for a salinity effect is gained by comparing ratios of average catch rates within the plume to rates outside the plume (table 3) with concurrent salinities (fig. 4) and salinity gradients (table 2) in the plume. Salinity and intensity of the plume are inversely ordered with catch-rate ratios (see rank columns in tables 2 and 3).

In summary, I suggest that higher temperatures within the plume, produced by relative constraint of heat, give rise to greater concentration of albacore within the plume province than beyond it once the fish move into the area off Oregon-Washington; plume salinity, to which temperature change is inversely related, qualifies the degree to which temperature difference can be effective (or even negates it during times of extremely low salinity, such as July 1964). Although the now unknown year-to-year differences in total abundance of albacore should be considered in this discussion, the degree to which the proposed mechanisms for differential distribution of albacore are supported by fishery data indicates that variation of albacore distribution over the study area may be as important as variation of total abundance in determining the yield of that fishery.

Results of this study indicate effects of variation of temperature and salinity on albacore distribution. At present experimental information is lacking on physiological and behavioral responses of albacore to such variations. Other factors may affect albacore and may themselves be related to variation of temperature and salinity: the role of forage in the plume province as an attractant to albacore may be worth investigating.

The commercial fishery for albacore off Oregon and Washington has extended infrequently to, and seldom beyond, the offshore limit of the plume province, in part because the range of Oregon-Washington fishing boats is generally short. Consequently, I believe that only a small fraction of the total albacore in the area considered has been exposed to fishing. Results of this work suggest that the fishery should be extended to the plume limits in most years and farther in years of high plume intensity. Confirmation of the hypothesis presented here will be necessary, as well as useful, by accumulation of more paired observations on plume and albacore distribution. Should the hypothesis be supported, areal differences in catch rate of albacore can be estimated from preseason geostrophic flow, wind field, and Columbia River discharge, because these factors largely determine the physical characteristics of the environment in this region.

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CALANOID COPEPODS FROM THE CENTRAL NORTH PACIFIC OCEAN

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ABSTRACT

A systematic study was made of the calanoid copepods in seven plankton samples collected between lat. 30°00′ N. and lat. 42°20′ N. along long. 155° W.

Sixty-four species belonging to 17 families are recorded. Measurements, descriptions, and illustrations are given for most of the species. Two species, *Euchirella unispina* and *Euchaeta wrighti*, are described as new, and the hitherto unknown female of *Centropages elegans* Giesbrecht is described for the first time. *Calocalanus tenuis* Farran is reported for the first time from the Pacific Ocean.

The systematics and distribution of the planktonic copepods of the North Pacific have been widely studied, but such investigations have largely been limited to peripheral waters. Outstanding are the papers by: Esterly (1905, 1906, 1911, 1913, 1924) and Davis (1949) for the eastern Pacific; by Mori (1937), Tanaka (1956a, 1956b, 1957a, 1957b, 1958, 1960, 1961, 1962, 1963, 1964a, 1964b, 1964c), and Vervoort (1946) for the western Pacific; by Brodsky (1950) for the northern North Pacific; and by Grice (1962) for the equatorial Pacific. The copepod fauna of the vast area of the open North Pacific, however, has been relatively little studied, although several early expeditions visited the area and yielded lists of local species (Dana, 1853, 1855; Brady, 1883; Giesbrecht, 1895; Wilson, 1942, 1950).

This paper is devoted to the systematic study of the calanoid copepods in plankton samples from the central North Pacific taken during cruise 29 of the research vessel *Hugh M. Smith* of the Bureau of Commercial Fisheries. Most of the laboratory work for the study was completed at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, in 1958 and 1959 under a fellowship from the International Cooperation Administration of the United States.

MATERIALS AND METHODS

The materials for this study consisted of seven plankton samples collected between lat. 30° 00′ N. and lat. 42° 20′ N. along long. 155° W. The samples were taken in oblique hauls with a 1-m. (mouth diameter) net. The front and middle sections of the net were made of 30XXX silk grit gauze (apertures averaging 0.65 mm. in width), and the rear section and bag of 56XXX silk grit gauze (apertures averaging 0.31 mm. in width). The hauls were from a depth of 140 m. and lasted about 30 minutes. The amount of water strained during each haul was measured by a flowmeter in the mouth of the net. The collecting methods for plankton samples adopted by the Biological Laboratory, Honolulu, have been described in detail by King and Demond (1953).

The pertinent data for each plankton sample are given in table 1. Hydrographic data obtained during *Hugh M. Smith* cruise 29 have been published by Graham (1957).

Only small quantities of the original samples were examined. Subsamples were obtained by using the Folsom Plankton Sample Splitter (McEwen, Johnson, and Folsom, 1954). The specimens of each species contained in the aliquot were counted to determine the numerical abundance of the common species. After I had completed the analysis of the subsample, I examined the remainder of the original sample for species not found in the aliquot or to obtain additional specimens, which were often needed to complete the description of a species. Table 2 shows the sizes of the subsamples examined, the list of species and the number of specimens

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TABLE 1. —*Data on plankton samples collected in the North Pacific Ocean, May 6–13, 1955*

[All samples from 140 m. to surface]

Station No.	Position	Date (1955)	Time (local time)	Water filtered
				Cubic meters
3	30°00′ N., 155°00′ W.	May 6	0756–0827	1457
5	31°54′ N., 154°49′ W.	May 7	0742–0818	2390
7	33°54′ N., 154°48′ W.	May 8	0722–0753	1674
9[1]	35°52′ N., 154°53′ W.	May 9	0707–0737	
13	38°23′ N., 154°51′ W.	May 11	0715–0748	1851
15	40°08′ N., 155°02′ W.	May 12	0721–0751	1844
16	42°20′ N., 154°57′ W.	May 13	0714–0744	1058

[1] The net was torn during the tow.

of each found in the aliquot, and the calculated number of copepods per cubic meter of water.

GENERAL REMARKS

The collections contained 64 species of calanoid copepods. Two species, *Euchirella unispina* and *Euchaeta wrighti*, were new. One species, *Calocalanus tenuis* Farran, 1926, had not been previously recorded from the Pacific Ocean. The hitherto unknown female of *Centropages elegans* Giesbrecht, 1895, was discovered and described.

The number of species increased from 14 at the northernmost station to 48 at the second southernmost. Except for *Clausocalanus arcuicornis*, none of the species occurred at all the stations. The common species toward the north-

TABLE 2.—*Species and number of specimens in each subsample of plankton*

"X" indicates the species found from collections in the North Pacific Ocean, May 6 13, 1955, in other fractions of original sample]

Species	Station number						
	3	5	7	9	13	15	16
1. *Calanus glacialis*		X	1	15	15	9	X
2. *C. pacificus*					X	8	12
3. *C. tenuicornis*	40	17	2	2	5	1	
4. *C. plumchrus*					24	66	376
5. *C. cristatus*					2	X	
6. *Nannocalanus minor*	76	85	6	18	1		
7. *Neocalanus gracilis*	14	30	11	50	6		
8. *N. robustior*	86	9	6				
9. *Eucalanus attenuatus*	X	X	X	X	13	10	
10. *E. elongatus*	10	18	24		34	8	
11. *E. bungii*		2	13		49	30	30
12. *Mecynocera clausii*		2	4	1			
13. *Paracalanus parvus*					1		
14. *Calocalanus pavo*		X	3				
15. *C. tenuis*					4		
16. *Pseudocalanus minutus*							1
17. *Clausocalanus arcuicornis*	100	7	14	8	38	6	6
18. *C. pergens*			1		1		
19. *Ctenocalanus vanus*		1	4	2	4	1	10
20. *Aetideus pacificus*							X
21. *Euaetideus acutus*	4	2	X	1			
22. *Euchirella truncata*	1	1	X	5	X		
23. *E. unispina* n. sp.	3	X	X	6			
24. *E. amoena*	2	X	X	1			
25. *E. rostrata*		12	1	18	3	6	
26. *Undeuchaeta plumosa*		X		7			
27. *Euchaeta marina*	2	X					
28. *E. spinosa*	5	6	X	6	X		
29. *E. media*		X		16	X		
30. *E. pubera*		1	X				
31. *E. wrighti* n. sp.	X						
32. *Phaenna spinifera*	X	X	1				
33. *Lophothrix latipes*	1	X	X				
34. *Scolecithrix danae*	16	2	X				
35. *S. bradyi*	X	X	X	1			
36. *Scolecithricella minor*							X
37. *S. dentata*		X				1	X
38. *S. ovata*		X	X				
39. *S. vittata*		X					
40. *S. auropecten*		3	1		1		
41. *Metridia lucens*							X
42. *Centropages bradyi*		X		1	38	13	
43. *C. elongatus*	20	X	X				
44. *C. violaceus*	X	X	2				
45. *C. elegans*	24	6	2				
46. *Lucicutia flavicornis*	8	X	X			X	1
47. *Heterorhabdus papilliger*		8	2	6	16	15	7
48. *H. abyssalis*				4			
49. *Heterostylites longicornis*		X	X				
50. *Haloptilus longicornis*	544	44	3				
51. *H. fertilis*	X	X					
52. *H. spiniceps*	12	X	X				
53. *Augaptilus spinifrons*		X					
54. *Arietellus aculeatus*	4						
55. *A. setosus*		X	X				
56. *Candacia ethiopica*	24	2	5	1			
57. *C. bipinnata*					6	6	X
58. *C. varicans*	4		X				
59. *C. longimana*	4	X	X				
60. *Paracandacia bispinosa*	144	20	1				
61. *Pontellopsis regalis*	X						
62. *Pontellina plumata*			X				
63. *Acartia danae*	4						
64. *A. negligens*	12	4	X				
Unidentified copepodids	26	8	6	21	75	9	14
Number of specimens in subsample	1,190	290	112	190	335	188	457
Subsample size	1/8	1/32	1/16	1/8	1/64	1/128	1/256
Number of copepods per cubic meter	6.5	3.9	1.1		11.6	13.1	110.6
Number of species	33	48	40	21	23	16	14

ern end of the area were *Calanus glacialis*, *C. pacificus*, *C. plumchrus*, *Eucalanus bungii*, *Ctenocalanus vanus*, *Heterorhabdus papilliger*, and *Candacia bipinnata*. The common species toward the southern end of the area were *Calanus tenuicornis*, *Nannocalanus minor*, *Neocalanus gracilis*, *N. robustior*, *Eucalanus elongatus*, *Euchaeta spinosa*, *Centropages elongatus*, *Haloptilus longicornis*, *Candacia ethiopica*, *Paracandacia bispinosa*, and *Acartia negligens*. *Euchirella rostrata* was fairly common in the area except at the extreme ends. *Euchaeta media* was common at one station and *Centropages bradyi* at two.

The calculated number of copepods per cubic meter of water varied from 1.1 at station 7 to 110.6 at the northernmost station (table 2). In comparison, Grice (1962) obtained 2.3 to 3.7 calanoids per cubic meter of water for tows at the surface and at 0 to 100 m. in the equatorial Pacific; however, he calculated a mean number of 26.8 copepods per cubic meter of water for depths between about 50 and 150 m. Brodsky (1952) reported a far greater abundance of copepods in the northwestern Pacific—5,040 per cubic meter of water for the 50- to 100-m. level, and 320 for the 100- to 200-m. level.

Of all the previous studies only Brady (1883) and Wilson (1942) reported planktonic copepods from the area under consideration. Brady listed the following nine species of calanoid copepods obtained in a surface plankton sample collected on July 21, 1875, from *Challenger* station 256 (lat. 30°22′ N., long. 154°56′ W.), which corresponds closely to station 3 of the present collections:

Undinula vulgaris
U. darwini
Euchaeta marina
Pleuromamma abdominalis
Centropages violaceus
Candacia truncata
Labidocera acutifrons
L. detruncata
Pontellopsis villosa

Of these only *Euchaeta marina* and *Centropages violaceus* were in the present collections. Of the remaining species, five were reported from the area by Wilson (1942), and two, *Pleuromamma abdominalis* and *Candacia truncata*, were obtained from equatorial waters by Grice (1962).

Wilson (1942) reported 48 species of calanoid copepods in plankton samples collected in early October in 0 to 100-m. tows at *Carnegie* stations 141–145 (between lat. 29°02′ N. and lat. 34°06′ N., and between long. 145°30′ W. and long. 160°44′ W.). These stations are in about the same area as the three southern stations of the present collections. Of the 48 species the following 26 were not in the present collections:

Megacalanus longicornis
**Canthocalanus pauper*
**Undinula vulgaris*
**U. darwini*
**Paracalanus aculeatus*
P. pygmaeus
Acrocalanus gibber
A. gracilis
**A. longicornis*
Calocalanus styliremis
Microcalanus pusillus
M. pygmaeus
**Clausocalanus furcatus*
**Euchirella curticauda*
**E. pulchra*
Euchaeta acuta
E. tonsa
**Centropages calaninus*
Lucicutia clausii
**Haloptilus acutifrons*
**Candacia simplex*
**Pontella tenuiremis*
Pontellopsis villosa
**Labidocera detruncata*
L. acutifrons
L. nerii

Most of these species are tropical or subtropical; 13 species (marked with an asterisk) were found by Grice (1962) in equatorial waters of the Pacific Ocean. If the difference in dates of collection is considered, seasonal changes may account for the absence of many tropical or subtropical copepods in the present collections that were reported in the two previous studies.

SYSTEMATIC ACCOUNT

The copepods were stained with methyl blue in lactic acid and dissected in lactic acid. All illustrations were made with a camera lucida. The total length was measured from the tip of the forehead to the ends of the caudal rami along a sagittal plane. The urosome was measured from the anterior margin of the genital segment to the ends of the caudal rami. These measurements excluded the telescoped portions of the segments. The proportional lengths of the urosomal segments, however, included the telescoped portions.

The anatomical terms used in the descriptions below are defined as follows: Cephalosome—the anterior portion of the body including the first anatomically thoracic segment bearing the maxillipeds. Metasome—the tagma composed of those thoracic segments normally bearing swimming legs; that is, the second to sixth anatomically thoracic segments. Prosome—the cephalosome and metasome, thus, the portion of the body anterior to the major articulation. Urosome—the portion of the body posterior to the articulation. In conformity with the prevailing convention, the perianal ring is counted as the last segment. The terminal urosomal structures may be fused into the so-called caudal furca, a complex composed of the perianal ring and the caudal rami, and sometimes an additional urosomal segment.

FAMILY CALANIDAE

Calanus finmarchicus s.l. Jashnov, 1955
(Plate 1, figs. 1–4)

Occurrence

Calanus glacialis

Sta. 5.	3 adult females, 3.45 to 3.84 mm.
Sta. 7.	7 adult females, 3.55 to 3.84 mm.
Sta. 9.	14 adult females, 3.55 to 3.79 mm.; 1 adult male, 3.10 mm.
Sta. 13.	19 adult females, 3.69 to 4.30 mm.; 2 adult males, 3.63 to 3.66 mm.
Sta. 15.	13 adult females, 3.40 to 3.84 mm.; 7 adult males, 3.20 to 3.70 mm.
Sta. 16.	1 adult female, 3.40 mm.

Calanus pacificus

Sta. 13.	6 adult females, 2.80 to 3.00 mm.
Sta. 15.	18 adult females, 2.73 to 3.01 mm.; 3 adult males, 2.67 to 2.80 mm.
Sta. 16.	18 adult females, 2.62 to 2.97 mm.; 8 adult males, 2.64 to 2.87 mm.

Remarks

C. finmarchicus s. l. has been extensively studied by Jashnov (1955, 1957a, 1957b, 1958, 1961), Brodsky (1948, 1950, 1959, 1962, 1965), and Grainger (1961). The specimens in the present collections can be divided into two size groups. The large form is identified with *C. glacialis* Jashnov, 1955, and the small form is probably referable to *C. pacificus* Brodsky, 1948.

C. glacialis is an arctic species, widely distributed in the polar basin and marginal seas (Jashnov, 1955; Grainger, 1961). This species has also been reported from the Sea of Okhotsk by Ponomareva (1961) but has not been previously recorded from the open Pacific Ocean.

The female of *C. glacialis* has a total length of 3.40 to 4.30 mm. The proportional lengths of the prosome and the urosome are about 3.5–3.7:1. The genital segment is wider than long (53:47), and the caudal ramus is 1.4 times longer than wide (fig. 1). The inner margin of the coxa of the fifth leg has a conspicuous concavity and 17 to 29 teeth (fig. 2). The third endopodal segment of the fifth leg has 5 or 6 setae.

The total length of female *C. pacificus* varies from 2.62 to 3.01 mm. The proportional lengths of the prosome and the urosome are about 3.28–3.47:1. The genital segment is slightly longer than wide (51:49), and the caudal ramus 1.6 times as long as wide (fig. 3). The coxa of the fifth leg has a conspicuous concavity and 24 to 36 teeth along the inner margin (fig. 4). The distal segment of the endopod of the fifth leg has 5 or 6 setae as does that of *C. glacialis*.

The males of the two forms are also readily distinguished from each other by size. Males of *C. glacialis* are 3.10 to 3.70 mm., those of *C. pacificus* 2.64 to 2.87 mm.

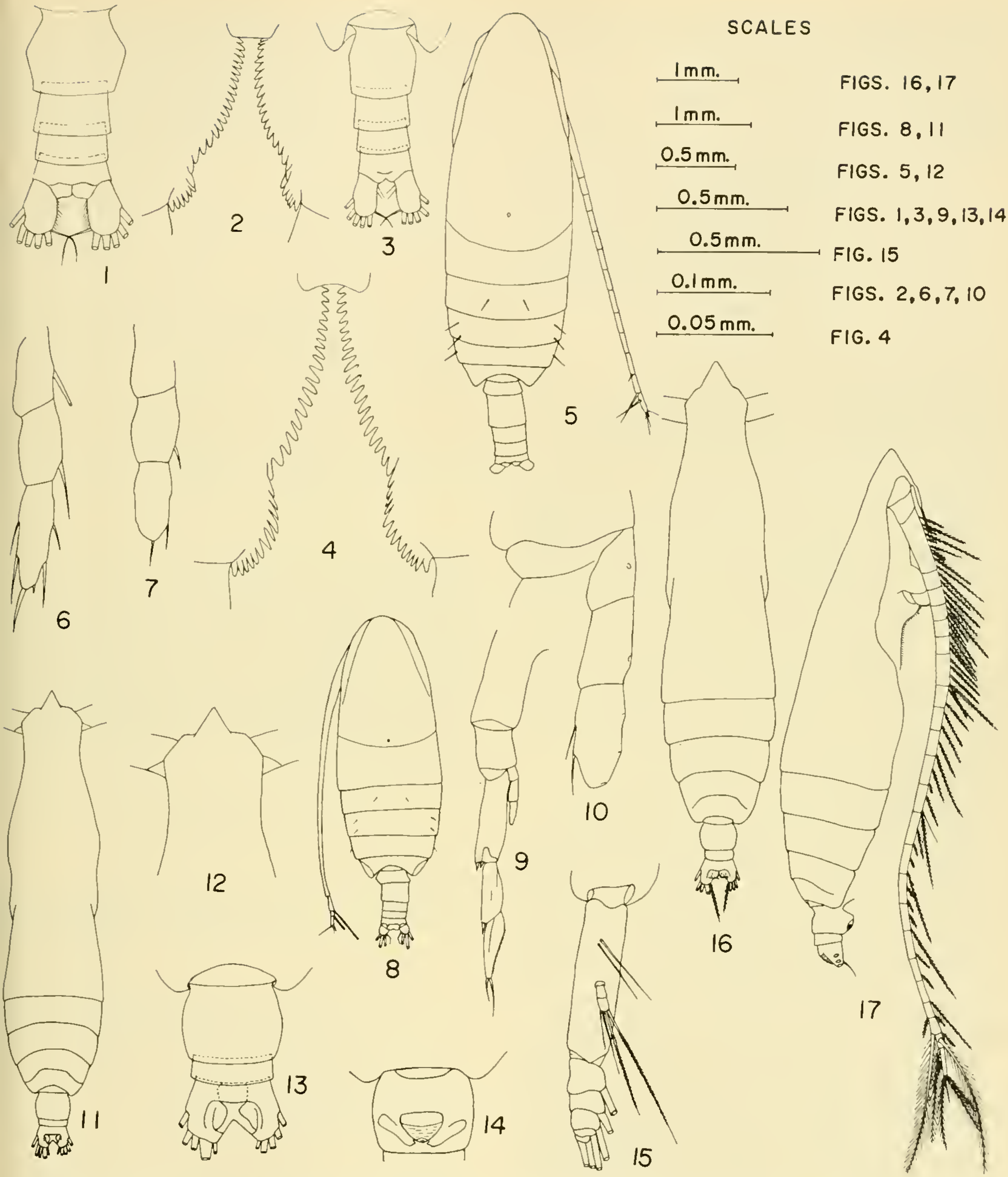
SCALES
1mm.
FIGS. 16,17
1mm.
FIGS. 8,11
0.5mm.
FIGS. 5,12
0.5mm.
FIGS. 1,3,9,13,14
0.5mm.
FIG. 15
0.1mm.
FIGS. 2,6,7,10
0.05mm.
FIG. 4
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Plate 1.—Figs. 1–2, *Calanus glacialis*. Female: fig. 1, urosome, dorsal view; fig. 2, inner margins of coxae of fifth pair of legs. Figs. 3–4, *Calanus pacificus*. Female: fig. 3, urosome, dorsal view; fig. 4, inner margins of coxae of fifth pair of legs. Figs. 5–7, *Neocalanus gracilis*. Male: fig. 5, habitus, dorsal view; figs. 6–7, endopods of left fifth legs. Figs. 8–10, *Neocalanus robustior*. Male: fig. 8, habitus, dorsal view; fig. 9, left fifth leg; fig. 10, endopod of left fifth leg. Figs. 11–15, *Eucalanus attenuatus*, small form. Female: fig. 11, habitus, dorsal view; fig. 12, forehead, dorsal view; fig. 13, urosome, dorsal view; fig. 14, genital segment, ventral view; fig. 15, mandibular palp. Figs. 16–17, *Eucalanus attenuatus*, large form. Female: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view.

The distal portions of the swimming legs were missing in all specimens.

Calanus tenuicornis Dana, 1849

Occurrence

Sta. 3. 10 adult females, 1.71 to 1.83 mm.
Sta. 5. 17 adult females, 1.68 to 2.04 mm.; 1 adult male, 1.88 mm.
Sta. 7. 13 adult females, 1.78 to 2.22 mm.
Sta. 9. 2 adult females, 1.90 to 1.98 mm.
Sta. 13. 5 adult females, 1.88 to 2.22 mm.
Sta. 15. 1 adult female, 1.91 mm.

Remarks

This species can easily be recognized by the elongate antennules and the absence of the hooked spiniform process on the anterior aspect of the basis of the first leg that appears in the species of *Neocalanus.*

Most of the present specimens, like those observed by Bowman (1955) and Grice (1962), had protozoan parasites in the caudal rami and the setae were consequently eroded.

Bowman (1955) found that specimens off the California coast included two different types of *C. tenuicornis* Dana that were distinguishable from each other mainly by their size. He created a new species, *C. lighti,* for the large and elongate form. The present collections have no specimen identifiable with *C. lighti.*

Calanus plumchrus Marukawa, 1921

Occurrence

Sta. 13. 24 fifth copepodids, 3.93 to 4.41 mm.
Sta. 15. 66 fifth copepodids, 3.84 to 4.03 mm.
Sta. 16. 376 fifth copepodids, 3.84 to 4.32 mm.

Remarks

The specimens of the present collections are identical with the fifth copepodid of *Calanus tonsus* Brady described by Campbell (1934), except that they are smaller than Campbell's (4.5–5.0 mm., from the Strait of Georgia) and have 8 setae, instead of 7, on the third endopodal segment of the third leg.

Tanaka (1956a), who compared adult specimens of *C. plumchrus* from the North Pacific with *C. tonsus* Brady from the Antarctic, reported that the two forms are not identical.

Calanus cristatus Krøyer, 1848

Occurrence

Sta. 13. 6 fifth copepodids, 6.1 to 6.8 mm
Sta. 15. 1 fifth copepodid, 6.1 mm.

Nannocalanus minor (Claus, 1863)

Occurrence

Sta. 3. 14 adult females, 1.70 to 2.20 mm.; 3 adult males, 1.55 to 1.88 mm.
Sta. 5. 75 adult females, 1.84 to 2.24 mm.; 10 adult males, 1.65 to 2.01 mm.
Sta. 7. 21 adult females, 1.81 to 2.07 mm.; 11 adult males, 1.71 to 1.88 mm.
Sta. 9. 15 adult females, 1.84 to 2.04 mm.; 3 adult males, 1.84 to 1.88 mm.
Sta. 13. 1 adult female, 2.21 mm.

Remarks

Sewell (1929) divided females of this species, mainly by size, into two different forms, namely f. *major* and f. *minor.* Later Sewell (1947) also recognized two forms of the male. I was unable to distinguish these forms among the present specimens.

Neocalanus gracilis (Dana, 1849)
(Plate 1, figs. 5–7)

Occurrence

Sta. 3. 8 adult females, 3.00 to 3.20 mm.
Sta. 5. 30 adult females, 3.16 to 3.46 mm.; 7 adult males, 2.80 to 2.83 mm.
Sta. 7. 16 adult females, 3.26 to 3.55 mm.; 5 adult males, 2.73 to 2.93 mm.
Sta. 9. 47 adult females, 3.26 to 3.74 mm.; 3 adult males, 2.83 to 3.06 mm.
Sta. 13. 6 adult females, 3.45 to 3.64 mm.

Remarks

In the male, the first metasomal segment is separate from the cephalosome. The distance between a small process on the dorsodistal surface of the cephalosome and the articulation between the cephalosome and the first metasomal segment is nearly equal to the length of the first metasomal segment (fig. 5). The endopod of the left fifth leg (fig. 6) is not as well developed as that of the fourth leg; in some specimens its setae are almost completely reduced (fig. 7).

Neocalanus robustior (Giesbrecht, 1888)
(Plate 1, figs. 8–10)

Occurrence

Sta. 3. 28 adult females, 4.03 to 4.32 mm.; 7 adult males, 3.16 to 3.45 mm.
Sta. 5. 7 adult females, 4.03 to 4.22 mm.; 11 adult males, 3.36 to 3.45 mm.
Sta. 7. 12 adult females, 4.12 to 4.41 mm.; 3 adult males, 3.36 to 3.55 mm.

Remarks

This species can easily be distinguished from *N. gracilis*—the female by its large size, the shape of the genital segment, and the shape of the external margin of the maxilla, and the male by the location of the small process at the dorsodistal margin of the cephalosome (fig. 8). The left fifth leg of the male (fig. 9) has a rudimental 3-segmented endopod, the distal segment of which, in some specimens, has 2 or 3 small setae (fig. 10).

FAMILY EUCALANIDAE

Eucalanus attenuatus (Dana, 1849)
(Plate 1, figs. 11–17; plate 2, figs. 1–16; plate 3, figs. 1–13)

Occurrence

Both small and large forms were taken.

Small form
Sta. 3. 1 adult female, 4.51 mm.;
1 fifth copepodid male, 3.55 mm.
Sta. 5. 2 adult females, 4.51 to 4.70 mm.;
1 fifth copepodid male, 3.64 mm.
Large form
Sta. 5. 1 fifth copepodid male, 5.56 mm.
Sta. 7. 3 adult females, 6.62 to 6.91 mm.;
1 fifth copepodid female, 5.66 mm.;
4 fifth copepodid males, 5.56 to 6.04 mm.
Sta. 9. 2 fifth copepodid females, 5.47 to 5.56 mm.;
1 fifth copepodid male, 5.47 mm.
Sta. 13. 5 adult females, 6.52 to 6.81 mm.;
25 fifth copepodid females, 5.56 to 6.14 mm.;
1 adult male, 6.00 mm.;
28 fifth copepodid males, 5.56 to 6.04 mm.
Sta. 15. 11 adult females, 6.52 to 7.00 mm.;
14 fifth copepodid females, 5.47 to 5.95 mm.;
17 fifth copepodid males, 5.56 to 6.04 mm.

The present collections have two forms of *E. attenuatus* differing from each other mainly in size of the body and in number of setae of the mandibular palp. The small form seems to agree in anatomical details with the description given by Giesbrecht (1892) to this species, but the large form apparently has not been described. Both forms are described below.

Small Form

The small form is described in less detail than the large form and mainly for comparison.

Description of Female

In a specimen 4.70 mm. long the proportions of the prosome to the urosome are about 7.2:1 (plate 1, fig. 11). Those of the 2 free urosomal segments and the caudal furca are 49:16:35 (plate 1, figs. 13 and 14). The genital segment is wider than long (55:45). The height of the produced, triangular part of the forehead (plate 1, fig. 12) is about four-fifths the length of the base. The mandibular palp (plate 1, fig. 15) has 2 setae on the basis, 4 setae on the second endopodal segment, and 6 setae on the exopod.

Description of Immature Male

Only 2 fifth copepodid males were found. These immature forms can readily be identified by the setal arrangement on the mandible, which is the same as that of the adult female.

Large Form

Detailed descriptions of adult females, fifth copepodid female, adult male, and fifth copepodid male follow.

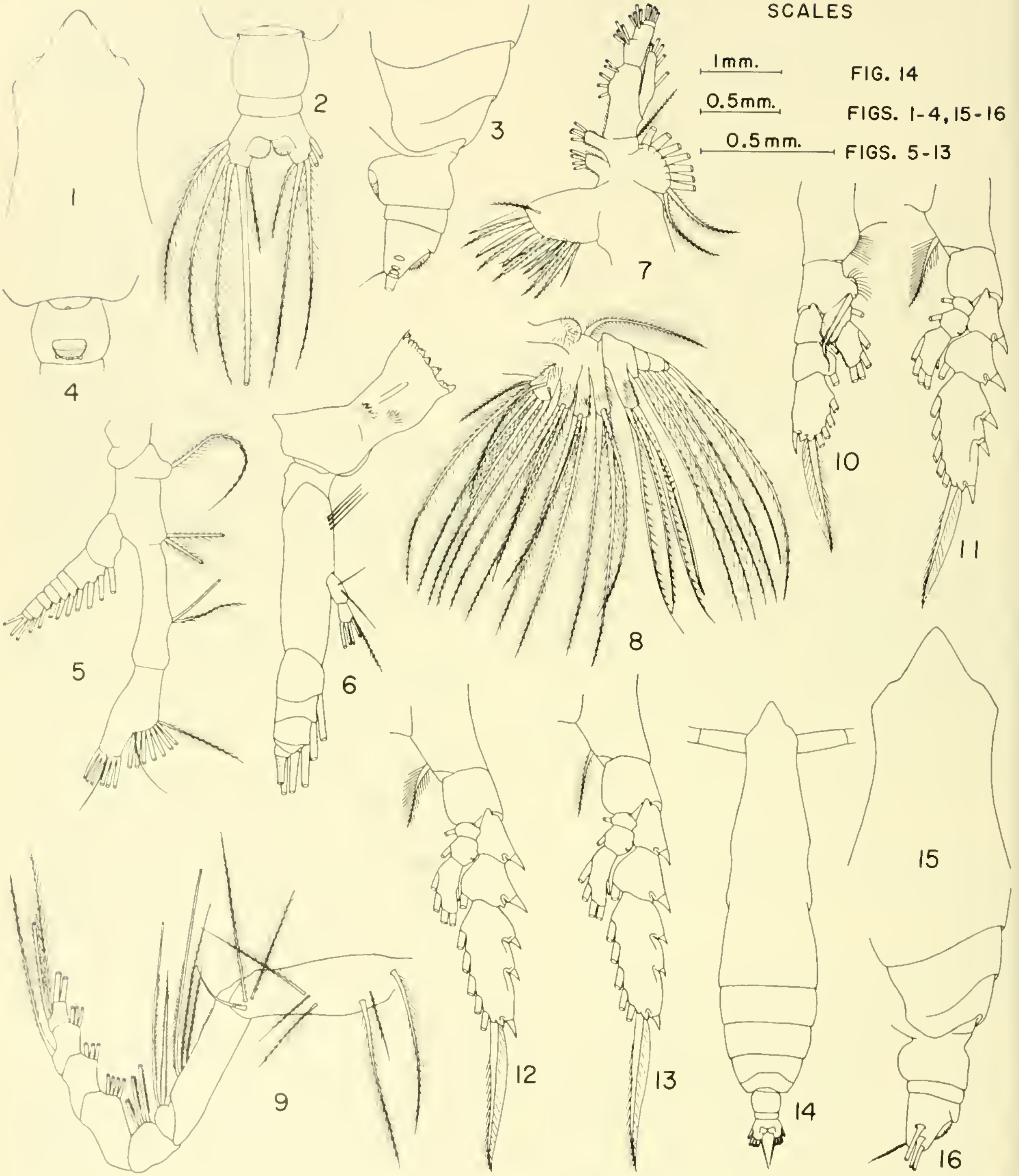
SCALES
1mm.
FIG. 14
0.5mm.
FIGS. 1-4,15-16
0.5mm.
FIGS. 5-13
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PLATE 2. Figs. 1–16, *Eucalanus attenuatus,* large form. Female: fig. 1, forehead, dorsal view; fig. 2, urosome, dorsal view; fig. 3, posterior part of metasome and urosome, lateral view; fig. 4, genital segment, ventral view; fig. 5, antenna; fig. 6, mandible; fig. 7, maxillule; fig. 8, maxilla; fig. 9, maxilliped; fig. 10, first leg; fig. 11, second leg; fig. 12, third leg; fig. 13, fourth leg. Fifth copepod females: fig. 14, habitus, dorsal view; fig. 15, forehead, dorsal view; fig. 16, posterior part of metasome and urosome, lateral view.

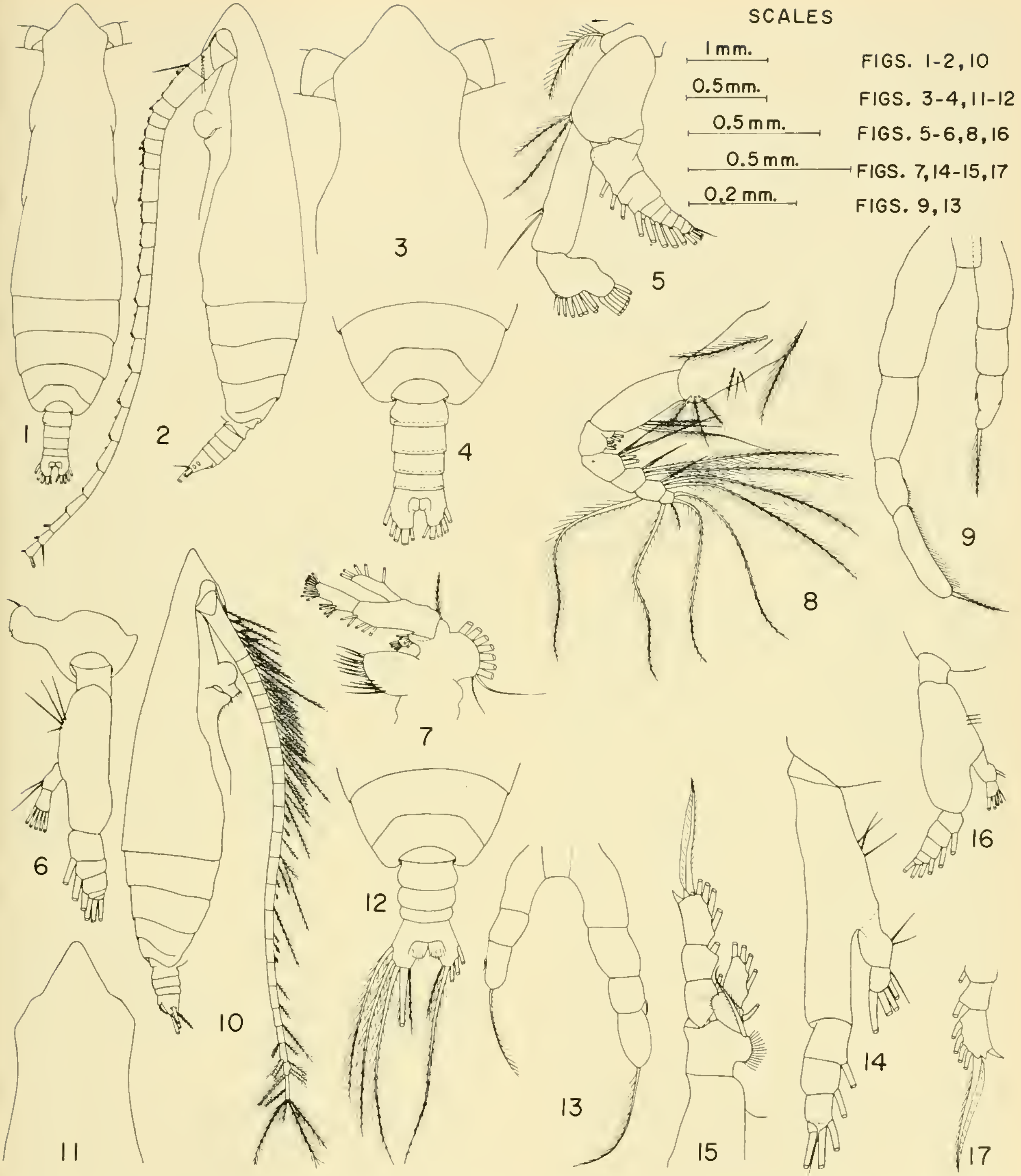
SCALES
1 mm. FIGS. 1-2, 10
0.5 mm. FIGS. 3-4, 11-12
0.5 mm. FIGS. 5-6, 8, 16
0.5 mm. FIGS. 7, 14-15, 17
0.2 mm. FIGS. 9, 13
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PLATE 3. Figs. 1–13, *Eucalanus attenuatus*, large form. Male: fig. 1, habitus, dorsal view; fig. 2, habitus, lateral view; fig. 3, forehead, dorsal view; fig. 4, posterior part of metasome and urosome, dorsal view; fig. 5, antenna; fig. 6, mandible; fig. 7, maxillule; fig. 8, maxilliped; fig. 9, fifth pair of legs. Fifth copepodid male: fig. 10, habitus, lateral view; fig. 11, forehead, dorsal view; fig. 12, posterior part of metasome and urosome, dorsal view; fig. 13, fifth pair of legs. Figs. 14–17, *Eucalanus elongatus*. Female: fig. 14, mandibular palp; fig. 15, first leg. Male: fig. 16, mandibular palp; fig. 17, exopod of first leg.

Description of Adult Female

The total lengths of 19 adult females range from 6.52 to 7.00 mm. The prosome is much longer than the urosome (plate 1, fig. 16), and the ratio of these two body parts is about 7.6:1. The anterior region of the head (plate 2, fig. 1) is markedly constricted in front of the antennules and is triangular in dorsal view; the height is about two-thirds the length of the base. The first metasomal segment is fused with the cephalosome. The fourth and fifth metasomal segments are not completely separated, but are fused in the ventrolateral regions (plate 2, fig. 3). The posterolateral corners of the metasome are smoothly rounded.

The urosome consists of 2 free segments and the compound caudal furca. The first or genital segment is composed of 2 fused segments, and the caudal furca is formed of 2 segments fused with the rami. The proportional lengths of the segments and caudal furca, from anterior to posterior, are 45:18:37.

The genital segment (plate 2, fig. 2) is wider than long (55:45); ventrally it projects in a round swelling, bearing the genital aperture (plate 2, figs. 3 and 4). The left caudal ramus is slightly larger than the right. The second medial terminal seta on the left ramus is markedly stouter and much longer than the others.

The antennule (plate 1, fig. 17) has 23 free segments; the first and second and the eighth and ninth segments are fused. The last 6 segments extend beyond the caudal rami. Each segment carries one or several strong plumose setae that are often reddish.

The exopod of the antenna (plate 2, fig. 5) is 8-segmented, has 12 setae, and reaches about the end of the first endopodal segment. The first endopodal segment is about 1.3 times as long as the second and has 2 setae along the inner edge, two-fifths the length of the segment from the distal end. The second endopodal segment has 8 long setae and 1 short seta on the internal lobe and 6 long setae and 1 short seta on the external lobe.

The mandibular palpus (plate 2, fig. 6) is 1.7 times as long as the mandibular blade and is biramous. The basis is more or less cylindrical and has 4 setae at the upper portion of the internal margin. The endopod arises from near the middle of the basis and is 2-segmented; the first segment has 2 short setae and the second 1 short seta and 4 long setae.

In the maxillule (plate 2, fig. 7), the first inner lobe has 15 spines, and each of the second and third inner lobes has 4 setae. The first outer lobe is rather small and has 9 setae. The second outer lobe is not pronounced and has a single plumose seta. The basis has 5 setae along the internal margin and carries laterally an exopod and distally an endopod. The exopod has 5 setae. The endopod is 3-segmented; the first 2 segments are partially fused and each has 4 setae, and the small apical segment has 5 setae.

The maxilla (plate 2, fig. 8) is well developed. The outer margin of the coxa has a round swelling with hairs. Next to the swelling is a markedly depressed portion from which arises a long, plumose seta. The various lobes are well developed. The first lobe has 6 setae and a small spine, each of the second to fourth lobes has 3 setae, the fifth lobe carries 3 setae and a long spine, and the sixth lobe has a single seta. In addition, the segments of the endopod have setae as follows: 1 on the first, 2 on the second, and 2 on the terminal segment.

The coxa of the maxilliped (plate 2, fig. 9) is composed of 4 lobes: the proximal lobe has 1 seta; the second, 2 setae; and the third and fourth lobes, 3 setae each. The basis has 3 setae just distad of the midpoint and 2 on the distal lobe. The endopod consists of 5 segments, which have 3, 4, 3, 3 + 1, and 2 + 2 setae, respectively.

The coxa of the first leg (plate 2, fig. 10) lacks setae, but its inner margin is fringed with hairs. The basis has a curved, plumose seta at the internal apex. The exopod is 3-segmented. The first and second segments are devoid of external spines, but each has 1 internal seta; the third segment has 1 external spine at the distal corner, a slender terminal spine, and 4 internal setae. The endopod is 2-segmented: the first segment has a single internal seta; the second segment 2 internal and 2 terminal setae.

The second to fourth legs (plate 2, figs. 11–13) are alike. The coxa has an internal plumose seta, but the basis lacks setae. Both the exopod and the endopod are 3-segmented. Each of the first and second exopodal segments has 1 strong external spine and 1 internal seta; the third segment has 3 external spines, 5 internal setae, and 1 slender terminal spine. Each of the first and second endopodal segments has 1 internal seta. The third segment has 1 external seta, 2 internal setae, and 2 terminal setae. The fifth pair of legs is lacking.

Description of Fifth Copepodid Female

The total lengths of 42 specimens range from 5.47 to 6.14 mm. The prosome is about 7.8 times as long as the urosome. The body shape (plate 2, figs. 14 and 15) resembles that of the adult female. The genital segment shows a distinct ventral swelling (plate 2, fig. 16), but is not so strongly swollen as that of the adult female, and lacks the genital opening.

The segmental composition of the antennule is exactly like that of the adult female. The setal arrangement appears to be the same. The antennae, masticatory appendages, and the swimming legs are all similar to those of the adult female, but the internal lobe of the second endopodal segment of the antenna has 7 long setae instead of 8, and the second to fourth endopodal segments of the maxilliped have 3, 2, and 3 setae instead of 4, 3, and 4.

Description of Adult Male

The adult male was described from a single specimen. The total length is 6.00 mm.; the ratio of the prosome to the urosome is about 6:1. The forehead in dorsal view (plate 3, figs. 1 and 3) is almost triangular, but the apex is smoothly rounded and much less produced than in the adult female. The first metasomal segment is fused with the cephalosome. The fourth and fifth metasomal segments are not completely separated, but are fused in the ventrolateral regions (plate 3, fig. 2). The posterolateral corners of the metasome are smoothly rounded.

The urosome (plate 3, fig. 4) consists of 4 free segments and the caudal furca, a complex composed of the anal segment fused with the caudal rami. The segments and caudal furca have the following proportional lengths, from anterior to posterior: 17:22:18:13:30.

The genital segment is slightly produced on the left side, and has a distinct genital operculum. The left caudal ramus is slightly larger than the right. The second medial terminal seta on the left ramus is markedly stouter and much longer than the others.

The antennule (plate 3, fig. 2) has 24 free segments, only the eighth and ninth of which are fused; the last 7 segments extend beyond the caudal furca. The antenna (plate 3, fig. 5) is very similar to that of the female but the basis is stouter.

The mandible (plate 3, fig. 6) differs from that of the female in two respects: it is smaller, and the mandibular blade is degenerated and has a single spinelike tooth. The basis has 4 setae at the upper portion of the internal margin, as does that of the female. The endopod arises just distad of the midpoint of the basis and has 2 setae on the first segment and 5 on the second segment.

The maxillule (plate 3, fig. 7), maxilla, and the maxilliped (plate 3, fig. 8) are much smaller than those of the adult female but resemble the latter in shape and in details of setal arrangement.

The first to fourth pairs of legs are nearly identical with those of the female. The left and right fifth legs (plate 3, fig. 9) are both uniramous. The left one is 4-segmented; the distal segment is tipped with a seta, and the last two segments are fringed with hairs along the inner margins. The segments in the left fifth leg have the proportional lengths of 39:21:14:26. The right fifth leg is also 4-segmented, but the last 2 segments are incompletely separated. The distal segment is tipped with a seta, and the third segment has a small spine on its inner edge. The right fifth leg is short—it reaches about the middle of the second segment of the left leg. The segments have the proportional lengths of 48:24:28 (third + fourth).

Description of Fifth Copepodid Male

The total length of 51 specimens ranges from 5.47 to 6.04 mm. The proportional lengths of the prosome and urosome are 7.7:1. The general body shape (plate 3, fig. 10) resembles that of the fifth copepodid female. The head in dorsal view (plate 3, fig. 11) has a triangular frontal part that ends in a blunt point. The urosome (plate 3, fig. 12) consists of 3 free segments and the caudal furca.

The antennule (plate 3, fig. 10) has 23 free segments. The first and second and the eighth and ninth segments are fused, as in the adult female and fifth copepodid female. The antennae, masticatory appendages, and the first to fourth pairs of legs are identical with those of the fifth copepodid female. The fifth pair of legs (plate 3, fig. 13) is not fully developed. The left one is 4-segmented; the third segment carries a small outer spine, and the distal segment is tipped with a long seta. The right fifth leg is 3-segmented; the distal segment is tipped with a long seta and has a small external spine.

Remarks

The two forms of *E. attenuatus* closely resemble each other in general anatomy but are clearly distinct in size of the body and in setation of the mandibular palp. The total length of the adult female is 4.51 to 4.70 mm. in the small form and 6.52 to 7.00 mm. in the large form. The mandibular palp of the large form has 4 setae on the basis, 2 setae on the first endopodal segment, and 5 setae on the second; the palp of the small form has 2 setae on the basis, no seta on the first endopodal segment, and 4 setae on the second.

The biological significance of the morphological differences shown by the large form cannot be evaluated on the basis of the materials on hand. A. Fleminger (personal communication), however, regards the large forms as ecophenotypic variants.

Eucalanus elongatus (Dana, 1849)
(Plate 3, figs. 14–17)

Occurrence

Sta. 3.	10 adult females, 5.95 to 6.40 mm.
Sta. 5.	17 adult females, 6.24 to 6.91 mm.; 1 fifth copepodid male, 4.80 mm.
Sta. 7.	23 adult females, 6.05 to 7.00 mm.; 1 adult male, 4.60 mm.
Sta. 13.	9 adult females, 6.14 to 6.72 mm.; 1 adult male, 4.70 mm.; 13 fifth copepodid males, 4.60 to 4.90 mm.
Sta. 15.	3 adult females, 6.30 to 6.70 mm.; 4 fifth copepodid males, 4.70 to 4.80 mm.

Remarks

Giesbrecht (1892) described three varieties of *E. elongatus*, namely, *hyalinus*, *inermis*, and *bungii*. Johnson (1938) raised *inermis* and *bungii* to the status of species. The specimens listed here are identical with *hyalinus* and are mainly characterized by the pointed posterolateral corners of the metasome. The mandible has 3 short setae on the proximal part of the basis and 4 long setae plus 1 short seta on the second endopodal segment (figs. 14 and 16). The third exopodal segment of the first leg has 1 external spine (figs. 15 and 17).

Eucalanus bungii Giesbrecht, 1892
(Plate 4, figs. 1–3)

Occurrence

E. bungii bungii Johnson, 1938

Sta. 16.	19 adult females, 5.51 to 6.08 mm.; 3 fifth copepodid females, 4.27 to 4.75 mm.; 4 fifth copepodid males, 4.27 to 4.56 mm.

E. bungii californicus Johnson, 1938

Sta. 5.	1 fifth copepodid female, 4.22 mm.; 1 fifth copepodid male, 4.12 mm.
Sta. 7.	4 adult females, 5.66 to 5.95 mm.; 3 fifth copepodid females, 4.22 to 4.51 mm.; 6 fifth copepodid males, 4.12 to 4.51 mm.
Sta. 13.	7 adult females, 5.70 to 6.40 mm.; 20 fifth copepodid females, 4.30 to 4.80 mm.; 22 fifth copepodid males, 4.00 to 4.30 mm.
Sta. 15.	20 adult females, 5.28 to 6.40 mm.; 2 fifth copepodid males, 4.20 to 4.40 mm.
Sta. 16.	4 adult females, 5.70 to 6.27 mm.

Remarks

Eucalanus bungii can be easily distinguished from *E. elongatus* by the rounded postero-

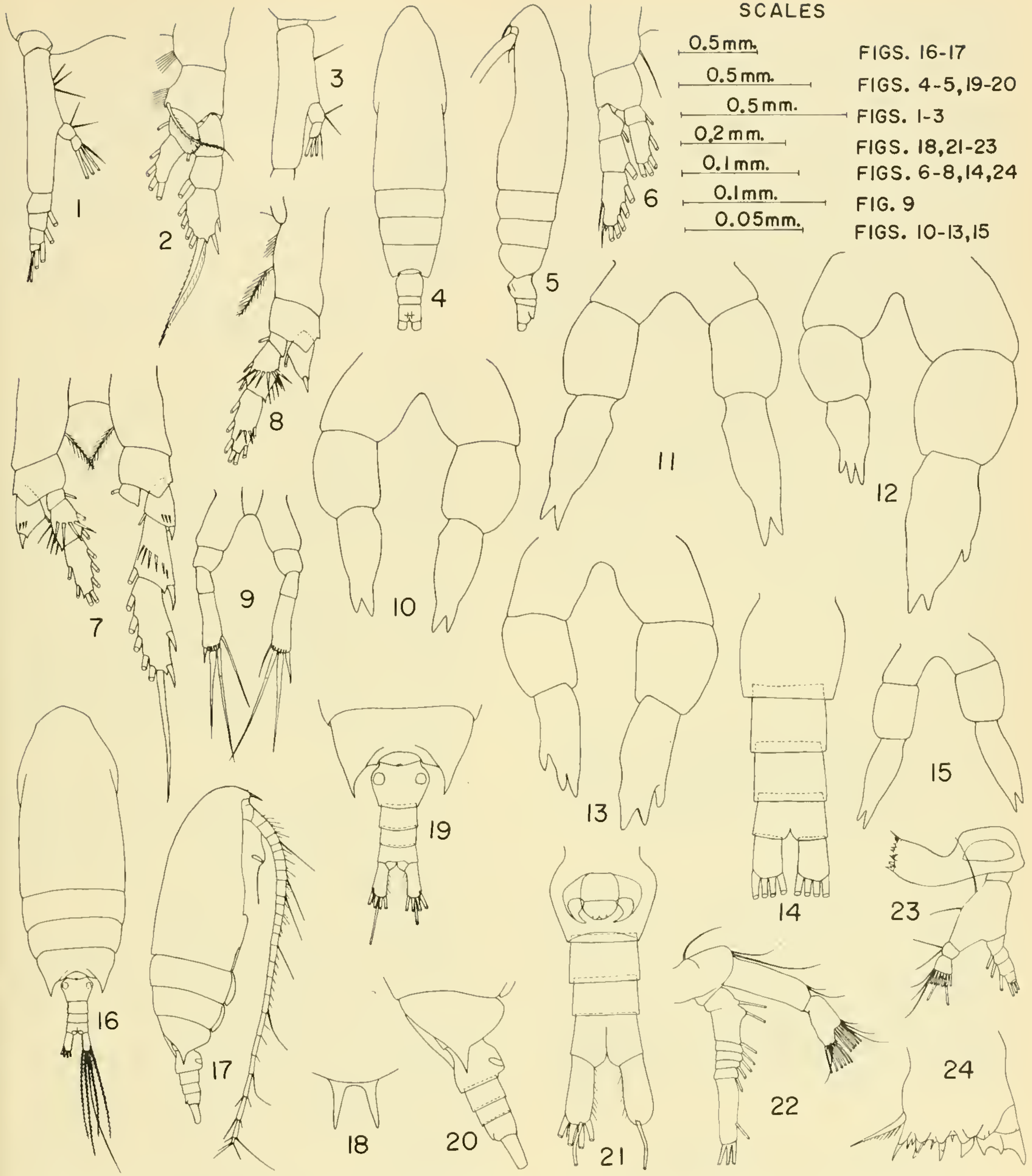
SCALES
0.5 mm. FIGS. 16-17
0.5 mm. FIGS. 4-5, 19-20
0.5 mm. FIGS. 1-3
0.2 mm. FIGS. 18, 21-23
0.1 mm. FIGS. 6-8, 14, 24
0.1 mm. FIG. 9
0.05 mm. FIGS. 10-13, 15
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PLATE 4. Figs. 1–3, *Eucalanus bungii*. Female: fig. 1, mandibular palp (*E. bungii bungii*); fig. 2, first leg (*E. bungii bungii*); fig. 3, mandibular palp (*E. bungii californicus*). Figs. 4–9, *Calocalanus tenuis*. Female: fig. 4, habitus, dorsal view; fig. 5, habitus, lateral view; fig. 6, first leg; fig. 7, second pair of legs; fig. 8, third leg; fig. 9, fifth pair of legs. Figs. 10–13, *Clausocalanus arcuicornis*. Female: fig. 10, fifth pair of legs, large form; fig. 11, fifth pair of legs, small form; figs. 12–13, abnormal fifth pairs of legs. Figs. 14–15, *Clausocalanus pergens*. Female: fig. 14, urosome, dorsal view; fig. 15, fifth pair of legs. Figs. 16–24, *Aetideus pacificus*. Female: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view; fig. 18, rostrum; fig. 19, posterior part of metasome and urosome, dorsal view; fig. 20, *idem*, lateral view; fig. 21, urosome, ventral view; fig. 22, antenna; fig. 23, mandible; fig. 24, cutting edge of mandibular blade.

lateral margins of the last metasomal segment and the presence of 2 external spines on the terminal exopodal segment of the first leg (fig. 2). By the setation of the mandibular palp, the specimens of the present collections can be divided into two forms that Johnson (1938) described as subspecies—*E. bungii bungii*, which has 3 setae on the basis of the palp (fig. 1), and *E. bungii californicus*, which has a single seta on this structure (fig. 3). Since these two forms are distinguishable from each other only on the basis of this apparently insignificant character, however, it seems better to recognize them as ecophenotypic variants than as subspecies.

Finding all possible transitions between Giesbrecht's (1892) varieties *hyalinus* and *bungii* in the *Snellius* plankton samples, Vervoort (1946) disagreed with Johnson's (1938) idea of elevating these varieties to specific level. The present materials, however, are in favor of Johnson's (1938) treatment in the absence of any intermediate forms.

Mecynocera clausii Thompson, 1888

Occurrence

Sta. 5. 4 adult females, 1.05 to 1.08 mm.; 1 fifth copepodid male, 0.99 mm.
Sta. 7. 5 adult females, 1.05 to 1.15 mm.; 2 fifth copepodid males, 0.99 mm.
Sta. 9. 1 adult female, 1.08 mm.

Remarks

This species can be recognized by the exceptionally long antennule, which is about twice as long as the body, and the comparatively small size of the copepod itself. According to T. Scott (1894), the fifth leg in both sexes of this species is 5-segmented. The three males in the present collections have 4-segmented fifth legs and 4-segmented urosomes, indicating that they are immature.

FAMILY PARACALANIDAE

Paracalanus parvus (Claus, 1863)

Occurrence

Sta. 13. 1 adult female, 1.00 mm.

Remarks

I find it curious that we took only one specimen of this reportedly cosmopolitan species.

Calocalanus pavo (Dana, 1849)

Occurrence

Sta. 5. 2 adult females, 1.08 to 1.12 mm.
Sta. 7. 10 adult females, 1.05 to 1.18 mm.

Remarks

Although widely distributed in the tropical and subtropical regions of all three great oceans, this species was found at only two of the stations.

Calocalanus tenuis Farran, 1926
(Plate 4, figs. 4–9)

Occurrence

Sta. 13. 4 adult females, 1.15 to 1.24 mm.

Description of Female

The body (figs. 4 and 5) is slender and fusiform; the anterior end of the cephalosome is vaulted. The cephalosome and the first metasomal as well as the fourth and fifth metasomal segments are completely fused. The urosome consists of 3 free segments and the caudal rami. The segments and caudal rami have the following proportional lengths, from anterior to posterior: 38:15:32:15. The genital segment is slightly broader than long in the proportions of 56:44. The caudal ramus is about as broad as it is long.

The first leg (fig. 6) has a 3-segmented exopod and a 2-segmented endopod. The coxa has a seta on the internal margin. The exopod has 0, 0, 2 external spines, 1, 1, 4 internal setae, and a terminal seta. The endopod has 1, 2 internal setae and 2 terminal setae.

The second leg (fig. 7) carries a plumose seta on the internal margin of the coxa. The 3-segmented endopod has 1, 2, and 7 setae, respectively. There are 4 spines, in a transverse row, on the posterior surface and 4 spines on the external margin of the second endopodal segment. The exopod is also 3-segmented, with 1, 1, 2 external spines and 1, 1, 5 internal setae in addition to a terminal seta. The posterior surfaces of the first and second exopodal segments carry 3 and 6 spines, respectively.

The endopod of the third leg (fig. 8) is 3-segmented. The segments have 1, 2, 7 setae, as does the endopod of the second leg. In addition, the second segment has 6 spines on the posterior surface and 4 spines on the external margin, and the third segment has 3 small spines on the posterior surface.

The fifth leg (fig. 9) is uniramous and 4-segmented. The segments have the proportional lengths of 35:13:17:35. The fourth segment has 1 distally situated external spine, 1 terminal spine, 2 distally situated internal setae, and a row of spinules at the bases of these spines and setae. As shown in figure 9, the right and left legs are different in the lengths of the external spines and the upper internal setae.

Remarks

Calocalanus tenuis was first described from the Bay of Biscay by Farran (1926) ; it has not been reported from the Pacific. The specimens in the present collections are poor, because some appendages are broken off. They are, however, readily recognized by the slender, fusiform body and the characteristic shape of the fifth leg.

FAMILY PSEUDOCALANIDAE

Pseudocalanus minutus (Kroyer, 1848)

Occurrence

Sta. 16. 1 adult female, 1.26 mm.

Clausocalanus arcuicornis (Dana, 1849)

(Plate 4, figs. 10–13)

Occurrence

Sta. 3. 7 large females, 1.51 to 1.60 mm.;
14 small females, 1.38 to 1.48 mm.;
2 males, 1.40 mm.
Sta. 5. 4 large females, 1.51 to 1.58 mm.;
3 small females, 1.12 to 1.41 mm.;
1 male, 1.28 mm.
Sta. 7. 6 large females, 1.50 to 1.55 mm.;
5 small females, 1.12 to 1.46 mm.
Sta. 9. 4 large females, 1.58 to 1.70 mm.;
3 small females, 1.28 to 1.50 mm.;
1 male, 1.42 mm.
Sta. 13. 7 large females, 1.65 to 1.83 mm.;
20 small females, 1.37 to 1.58 mm.;
1 male, 1.23 mm.
Sta. 15. 5 large females, 1.68 to 1.83 mm.;
21 small females, 1.20 to 1.51 mm.;
1 male, 1.14 mm.
Sta. 16. 5 small females, 1.28 to 1.31 mm.;
1 male, 1.46 mm.

Remarks

Sewell (1929), who studied material from the Indian Seas, divided females of *C. arcuicornis* into two forms, namely f. *minor* and f. *major*, mainly differing in the structure of the fifth pair of legs and the proportional lengths of the prosome and urosome. Grice (1962) found two female forms of this species in the equatorial Pacific and tentatively identified these with the two forms described by Sewell (1929). The females of the present collection also fall into two groups that are separable mainly by the total lengths and the shapes of the fifth pairs of legs.

The total lengths of the large form range from 1.50 to 1.83 mm. The prosome is 2.7 to 3.1 times as long as the urosome. In the fifth leg (fig. 10), the proximal segment is stouter and is longer than or as long as the following segment, and the terminal segment is shorter than the preceding two segments combined. The general shape of the fifth pair of legs is similar to that of f. *major* described by Sewell (1929), but my specimens are much larger than the 1.17 mm. reported by him.

The total length of the small form is 1.12 to 1.58 mm. The proportional lengths of the prosome and urosome are about equal to those in the large form. The proximal segment of the fifth leg (fig. 11) is slightly narrower and is shorter than the following segment. The terminal segment is longer than or as long as the preceding two segments combined. This small form seems to correspond to f. *major* described by Grice (1962) in total length and shape of the fifth pair of legs, but is not identical with Sewell's *major* in shape of the fifth pair of legs.

Two females from station 9 had abnormal fifth pairs of legs (figs. 12 and 13).

Clausocalanus pergens Farran, 1926

(Plate 4, figs. 14 and 15)

Occurrence

Sta. 7. 1 adult female, 0.85 mm.
Sta. 13. 1 adult female, 0.94 mm.

Remarks

This species can be distinguished from *C.*

arcuicornis mainly by its smaller size and other, minor, differences. The prosome is 2.5 to 2.8 times as long as the urosome. The caudal ramus (fig. 14) is longer than wide (63:37). The segments of the fifth leg (fig. 15) have the proportional lengths of 21:29:50, from proximal to distal.

Ctenocalanus vanus Giesbrecht, 1888

Occurrence

Sta. 5. 2 adult females, 1.06 to 1.08 mm.
Sta. 7. 6 adult females, 1.08 to 1.13 mm.
Sta. 9. 2 adult females, 1.14 mm.
Sta. 13. 4 adult females, 1.08 to 1.17 mm.
Sta. 15. 1 adult female, 1.26 mm.
Sta. 16. 5 adult females, 1.26 to 1.28 mm.; 5 fifth copepodid males, 1.26 to 1.28 mm.

Remarks

This species was at all the stations except the southernmost, although not in large numbers. It can easily be recognized by the ctenoid form of the external spines of the third exopodal segment of the third and fourth legs.

FAMILY AETIDEIDAE

Aetideus pacificus Brodsky, 1950

(Plate 4, figs. 16–24; plate 5, figs. 1–7)

Occurrence

Sta. 16. 5 adult females, 2.21 to 2.30 mm.

A complete description is given here because Brodsky's original description is brief and seems to disagree in some anatomical details with the present specimens.

Description of Female

The total lengths of five adult females range from 2.21 to 2.30 mm. The prosome is about 3.4 times as long as the urosome. The general outline of the prosome is ovate. In dorsal aspect the greatest width is at the fusion of the cephalosome and the first metasomal segment (plate 4, fig. 16). The first metasomal segment is completely fused with the cephalosome. The fourth and fifth metasomal segments are also completely fused. The cephalosome in dorsal aspect is slightly dilated in the oral region and is smoothly rounded anteriorly. The rostrum consists of two rather slender processes (plate 4, fig. 18).

The posterolateral corners of the metasome are produced into acute points, which in dorsal view are slightly curved inward (plate 4, fig. 19) and in lateral aspect point straight backward (plate 4, fig. 20). These points do not reach the distal margin of the genital segment in either dorsal or lateral view.

The urosome (plate 4, figs. 19–21) is 4-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 31:17:14:13:25. The genital segment in dorsal aspect is slightly wider than long (29:25) and has broadly rounded sides. The caudal rami are about 2.5 times as long as broad, and have 4 terminal setae of subequal length, a long ventral seta that is longer than the terminal setae, and a short external seta.

The antennule is 24-segmented; when it is applied against the body, its last 2 segments extend beyond the end of the caudal ramus (plate 4, fig. 17).

The endopod of the antenna (plate 4, fig. 22) is slightly shorter than the exopod. The first endopodal segment is styliform and has 2 setae almost at the distal end of the internal margin. The second endopodal segment is about half the length of the first and has 6 + 1 setae on the external lobe and 8 setae on the internal lobe. The first and second exopodal segments are incompletely separated; the former has no setae, but the latter has 2 setae proximally along the internal margin and 1 seta at the distal end of that margin. The third to sixth segments are fully separated; each has a strong seta. The seventh segment is elongate and has an internal seta at about two-thirds the length of the segment from the proximal end, and 3 apical setae.

The mandibular palp (plate 4, fig. 23) has a squarish basis with 2 setae along the internal margin. The endopod is 2-segmented and has 2 setae on the first segment and 9 + 2 on the second. The exopod is 5-segmented; each of the proximal 4 segments has a strong seta, and the distal segment 2 apical setae. The cutting edge of the mandibular blade (plate 4, fig. 24) is armed with about six groups of teeth and a basal seta.

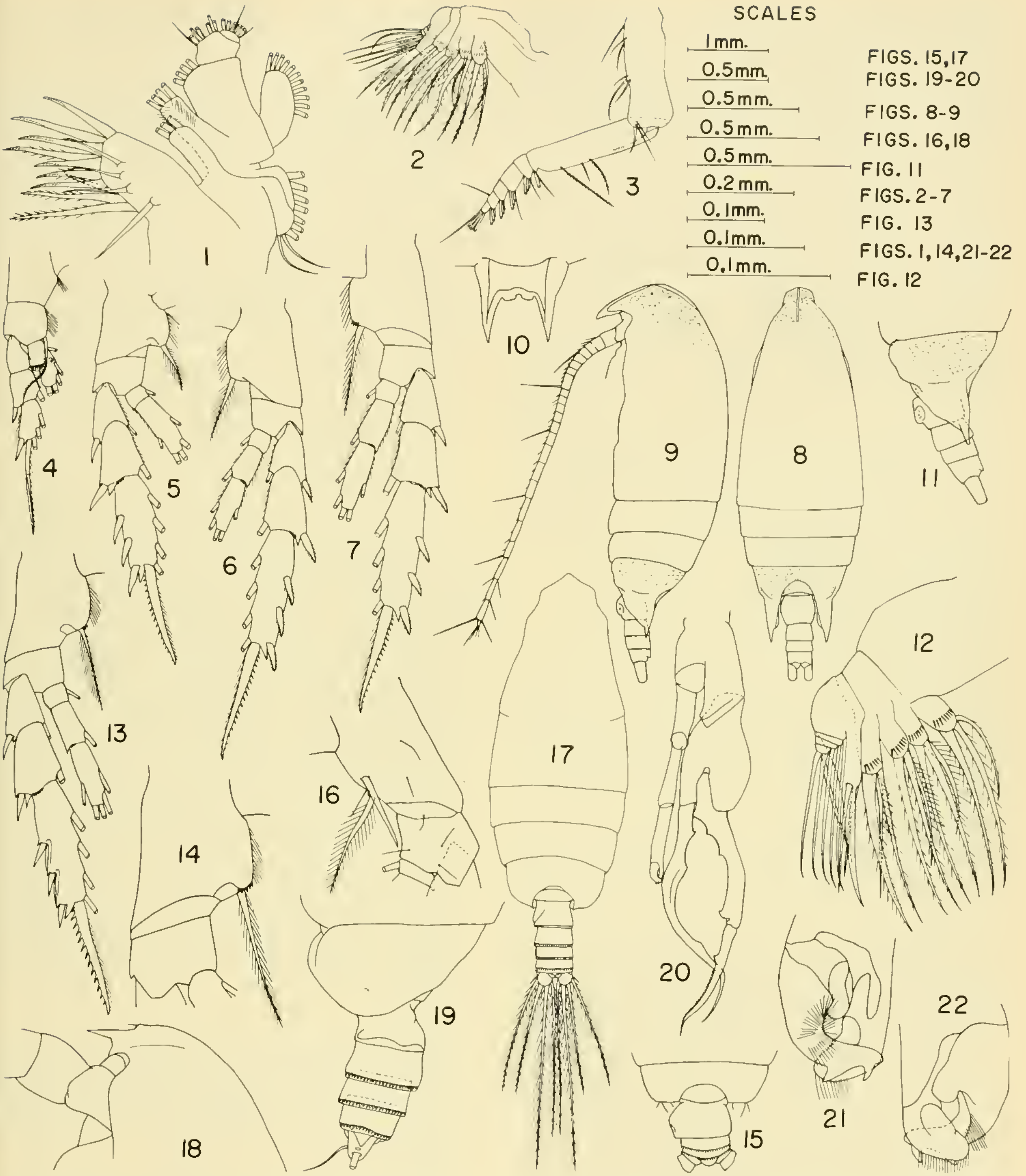
SCALES
1mm. FIGS. 15,17
0.5mm. FIGS. 19-20
0.5mm. FIGS. 8-9
0.5mm. FIGS. 16,18
0.5mm. FIG. 11
0.2mm. FIGS. 2-7
0.1mm. FIG. 13
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Plate 5. Figs. 1–7, *Actideus pacificus*. Female: fig. 1, maxillule; fig. 2, maxilla; fig. 3, maxilliped; fig. 4, first leg; fig. 5, second leg; fig. 6, third leg; fig. 7, fourth leg. Figs. 8–14, *Euaetideus acutus*. Female: fig. 8, habitus, dorsal view; fig. 9, habitus, lateral view; fig. 10, rostrum; fig. 11, posterior part of metasome and urosome, lateral view; fig. 12, maxilla; fig. 13, fourth leg; fig. 14, basipod of fourth leg. Figs. 15–22, *Euchirella truncata*. Female: fig. 15, posterior part of metasome and urosome, dorsal view; fig. 16, basipod of fourth leg. Male: fig. 17, habitus, dorsal view; fig. 18, forehead, lateral view; fig. 19, posterior part of metasome and urosome, lateral view; fig. 20, fifth pair of legs, posterior aspect; fig. 21, terminal part of left fifth leg, posterior aspect; fig. 22, *idem*, anterior aspect.

The maxillule (plate 5, fig. 1) is well developed. The first inner lobe has 9 strong spines along the internal margin, 4 relatively small spines on the posterior surface, and 1 small spine on the anterior surface. The second and third inner lobes are elongate and have 3 and 4 setae, respectively. The first outer lobe is low and has 9 setae. The basis bears 4 setae at the apex of the internal margin. The exopod has 11 setae. The endopod is 2-segmented, and carries 4 + 3 setae on the first segment and 6 + 2 setae on the second.

The maxilla (plate 5, fig. 2) has 5 well-developed lobes. Each of the first to fourth lobes bears 2 spiniform, spinulose setae of equal length, a short spinulose seta, and a few small spinules near the insertions of the setae. One of the 2 spiniform setae on the fourth lobe is much stouter than the other. The fifth lobe carries a strong dagger-shaped spine in addition to 2 slender setae. The endopod has 6 setae—1 on each of the proximal 3 segments and 3 on the terminal segment.

The maxilliped (plate 5, fig. 3) consists of a long basipod and a short endopod. The coxa has three groups of 3 setae each and is about as long as the basis, which has a row of spinules proximally, 3 scattered setae distally, and 2 setae at the extreme apex. The endopod has 5 segments, which have the following numbers of setae, from proximal to distal: 4, 4, 3, 3 + 1, and 4.

The first pair of legs (plate 5, fig. 4) has 3-segmented exopods and 1-segmented endopods. The coxa has no setae, but bears hairs along the proximal portion of the internal margin. The internal margin of the basis is fringed with hairs and has a curved seta at the distal end. The first exopodal segment lacks setae or spines. The second exopodal segment has an internal seta and an external spine. The internal margin of the spine appears to be slightly denticulate. The third exopodal segment has an external spine with a slightly denticulate internal margin. In addition, the segment has 3 internal setae and a long terminal spine, which has a lamella along the external margin and a row of hairs along the internal margin. Halfway along its external margin the endopod has a round tubercle which has a transverse row of small, acute spinules. In addition, the endopod has 3 internal setae, 2 terminal setae, and some small spinules at the base of the middle internal seta.

The coxa of the second leg (plate 5, fig. 5) has a considerably curved internal margin, which has a row of hairs and a short, thick seta. The basis has no hairs or setae. The exopod is 3-segmented. Each of the first and second segments has an external spine and an internal seta. In anterior aspect a row of small spinules lies along the distal border of the second segment. The third segment has 3 external spines, 4 internal setae, and a dagger-shaped terminal spine armed with 17 triangular teeth. The endopod is 2-segmented, with 1 seta on the first and 5 setae on the second segment, and reaches to about the distal border of the second exopodal segment.

The basipod and exopod of the third leg (plate 5, fig. 6) are similar to those of the second leg, but the external spines of the exopod are fringed with fine hairs and the terminal spine is armed with 19 acute, triangular teeth. The endopod is 3-segmented, with 1 seta on each of the first and second segments and 5 setae on the third, and extends slightly beyond the distal border of the second exopodal segment. A row of very fine spinules lies along the distal border of the second endopodal segment.

The fourth leg (plate 5, fig. 7) differs from the third in the following particulars: About 4 small, acute spines are at the insertion of the seta on the coxa. The endopod is longer, reaching to a line including one-third of the length of the third exopodal segment. The terminal spine is also absolutely shorter, and armed with 18 teeth along the external edge. The fifth pair of legs is absent.

Remarks

The armature of the mandibular blade of the present specimens disagrees with the original description of the species by Brodsky (1950) but agrees with his description for *Actideus armatus*.

I recently compared female specimens of *A. armatus* and *A. pacificus* from the Pacific coast of North America and found that, although the species are alike in anatomical details of the appendages, they are clearly distinguishable from each other by the size and general shape of the body. *A. armatus* is 1.80 to 2.02 mm. total length (about 50 specimens) and has metasomal processes that extend beyond the distal end of the genital segment. *A. pacificus*, as described above, has a slender body of 2.20 to 2.43 mm. (seven specimens) and has metasomal processes that do not reach the distal end of the genital segment. The male of *A. pacificus* is not known.

Euaetideus acutus (Farran, 1929)
(Plate 5, figs. 8–14)

Occurrence

Sta. 3. 3 adult females, 1.65 to 1.68 mm.
Sta. 5. 5 adult females, 1.68 to 1.78 mm.
Sta. 7. 1 adult female, 1.65 mm.

Sta. 9. 1 adult female, 1.68 mm.

Remarks

The female of this species can easily be distinguished by the following characters: The rostrum is very heavy and, in dorsal aspect, distinctly set off from the remainder of the head (fig. 8); the rami (fig. 10) are separated by a deep, U-shaped incision, at the base of which are two small knobs; the posterolateral corners of the metasome are produced into acute points that extend slightly beyond the distal border of the second urosomal segment (fig. 11); the dorsum of the prosome (figs. 8 and 9) has a pitted structure that is particularly visible at the forehead and on the last segment.

The antennae and the mouth parts were figured and described in detail by Vervoort (1957). The present specimens generally agree with his description except for the maxilla. The dagger-shaped spines on the fourth and fifth lobes of the maxilla (fig. 12) are almost identical in diameter, but different in length—the one on the fourth lobe is the longer. Each of the first to fourth lobes has a row of acute spinules, instead of irregular rows of spinules.

The first to fourth pairs of legs in general agree with those figured by Vervoort (1957). Some additional characters in the present specimens are as follows: In stained specimens, a line of demarcation is clearly visible between the first and second endopodal segments of the second leg. A row of fine spinules lies along the distal border of the second exopodal segment in the second to fourth legs and on the distal border of the second endopodal segment in the third to fourth legs. The coxa of the fourth leg has about 5 acute spinules at the insertion of the internal seta (figs. 13 and 14).

Euchirella truncata Esterly, 1911
(Plate 5, figs. 15–22)

Euchirella truncata Esterly, 1911, p. 322; plate 26, fig. 5; plate 28, fig. 35; plate 29, fig. 63; plate 30, fig. 71; plate 31, fig. 104.

Euchirella propria Esterly, 1911, p. 321, plate 27, figs. 14 and 20; plate 30, figs. 67 and 83; plate 31, fig. 85.

Occurrence

Sta. 3. 1 adult female, 5.40 mm.
Sta. 5. 5 adult females, 5.56 to 6.06 mm.; 1 adult male, 4.60 mm.
Sta. 7. 5 adult females, 5.85 to 6.24 mm.; 7 adult males, 4.60 to 5.08 mm.
Sta. 9. 2 adult females, 5.71 to 6.14 mm.; 3 adult males, 4.89 to 4.99 mm.
Sta. 13. 1 adult female, 6.81 mm.

Euchirella truncata was originally described by Esterly (1911) from females obtained in the San Diego, Calif., region of the eastern Pacific. As suggested by Vervoort (1963), *Euchirella propria*, erected on males alone by Esterly (1911), seems to be synonymous with *E. truncata*, for in the present study the two forms were found in the same samples and were closely similar in size as well as in anatomical details.

E. truncata has also been recorded from the South Atlantic as *E. gracilis* (Wolfenden, 1911), from the North Atlantic as *E. intermedia* (With, 1915), and from the Gulf of St. Lawrence as *E. acadiana* (Willey, 1919).

Description of Female

The female can easily be recognized by the shape of the genital segment, which is more swollen on the left side (fig. 15), and by the presence of a single strong spine on the coxa of the fourth leg (fig. 16).

Description of Male

The total length ranges from 4.60 to 5.08 mm. The prosome is about 4.2 times as long as the urosome. The cephalosome and the first metasomal segment as well as the fourth and fifth metasomal segments are fused (fig. 17). The forehead is smoothly rounded and has a strong rostrum (fig. 18). The posterolateral margins of the metasome are rounded (fig. 19).

The urosome consists of 5 free segments and the caudal rami which have the following proportional lengths, from anterior to posterior: 23:22:18:19:6:12. The last segment is almost completely telescoped into the fourth segment. The caudal rami are as long as they are wide. The distal margins of the second to fourth segments are each fringed by a row of small triangular spinules.

The uniramous left fifth leg (fig. 20) consists of 5 segments, the third of which reaches as far as the distal end of the basis of the right leg. The distal segment is small and inserted a short distance before the end of the fourth segment; the two segments together thus form a chela (figs. 21 and 22). Distally on the last segment are 2 teeth, which are curved outward. The right fifth leg consists of a well-developed, 2-segmented basipod, a 2-segmented exopod, and a 1-segmented endopod. The first exopodal segment bears 4 triangular processes along the internal margin—3 on the proximal half, and 1 near the distal end of the margin. The distal segment has a triangular process along the internal margin, at about one-third the length from the proximal end, and a row of small teeth distal to the process. The endopod is S-shaped and has 3 triangular processes along the external margin.

Euchirella unispina, new species

(Plate 6, figs. 1–21; plate 7, figs. 1–11)

Occurrence

Sta. 3. 6 adult females, 4.28 to 4.56 mm.
Sta. 5. 7 adult females, 4.60 to 4.70 mm.; 1 adult male, 3.84 mm.
Sta. 7. 3 adult females, 4.70 to 4.80 mm.; 1 adult male, 3.93 mm.
Sta. 9. 3 adult females, 4.60 to 4.89 mm.; 3 adult males, 3.93 to 4.03 mm.

Description of Female

The total length is from 4.28 to 4.89 mm. The prosome is about 4.3 times longer than the urosome. The first metasomal segment is fused with the cephalosome, but a line of demarcation is often visible in stained specimens. The fourth and fifth metasomal segments are completely fused. The forehead in dorsal aspect (plate 6, fig. 1) is slightly triangular and in lateral aspect (plate 6, fig. 2) smoothly curved into a powerful rostrum. The rostrum is single, points forward, and has an acute apex. The base of the rostrum has a distinct constriction from which 2 sensory hairs arise.

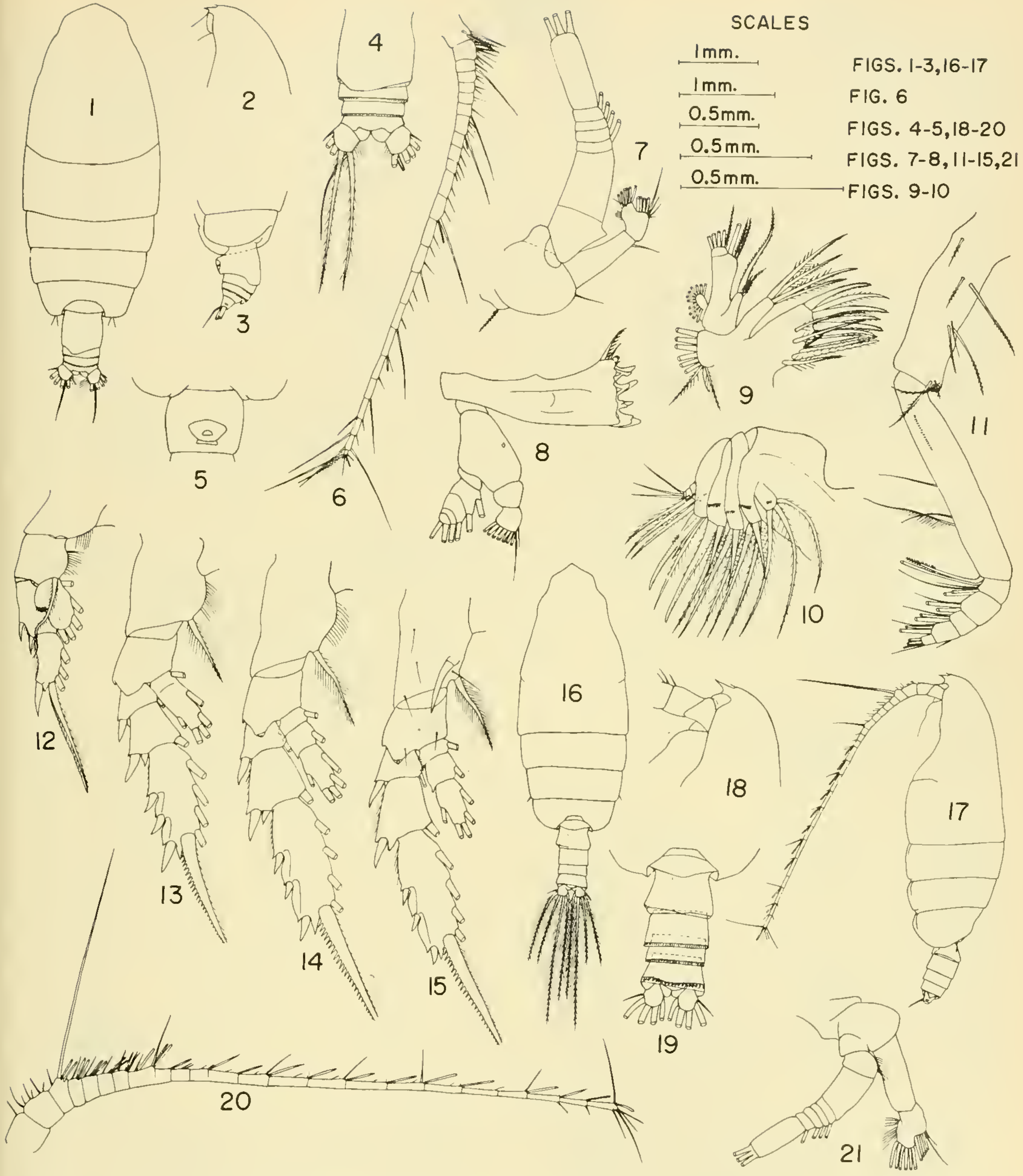
The posterolateral margins of the metasome are rounded. The urosome (plate 6, figs. 3–5) is 4-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 51:12:12:11:14. The genital segment is about as long as it is wide and slightly asymmetrical in dorsal aspect, as it is produced distally on the left side. The caudal rami are wider than long (24:19) and have 4 strong, subequal terminal setae, a short, strong external seta, and a curved internal seta.

The 24-segmented antennule reaches the end of the caudal ramus when folded back. The arrangement of the various setae and the aesthetes is illustrated in plate 6, figure 6.

The antenna (plate 6, fig. 7) has a short endopod, about equal to the first 2 exopodal segments combined. The first endopodal segment has 1 seta near the distal end of the internal margin, and the second endopodal segment has 8 setae on the internal and 6 + 1 setae on the external lobe. The exopod is 7-segmented; the proximal segment is produced into a triangular process near the distal end of the internal margin. Each of the 4 intermediate segments has 1 strong, plumose seta, and the elongate distal segment has 3 apical setae.

The cutting edge of the mandibular blade (plate 6, fig. 8) is armed with five groups of strong teeth and 2 basal spines. The posterior surface of the basis has a small process. The endopod is 2-segmented; the first segment lacks setae, but the second segment bears 9 apical setae. The exopod is 5-segmented, the segments together having 6 setae.

In the maxillule (plate 6, fig. 9), the first inner lobe is elongate, and has 12 strong spines plus 1 small spine. The second and third inner lobes are well developed; the second has 4 setae of subequal length and the third 1 large plus 2 small setae. The first outer lobe is low and has 8 setae. The basis is elongate and has 1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FIGS. 1-3,16-17
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FIG. 6
0.5mm.
FIGS. 4-5,18-20
0.5mm.
FIGS. 7-8,11-15,21
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FIGS. 9-10
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Plate 6. Figs. 1–21, *Euchirella unispina*, new species. Female: fig. 1, habitus, dorsal view; fig. 2, forehead, lateral view; fig. 3, posterior part of metasome and urosome, lateral view; fig. 4, urosome, dorsal view; fig. 5, genital segment, ventral view; fig. 6, antennule; fig. 7, antenna; fig. 8, mandible; fig. 9, maxillule; fig. 10, maxilla; fig. 11, maxilliped; fig. 12, first leg; fig. 13, second leg; fig. 14, third leg; fig. 15, fourth leg. Male: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view; fig. 18, forehead, lateral view; fig. 19, posterior part of metasome and urosome, dorsal view; fig. 20, left antennule; fig. 21, antenna.

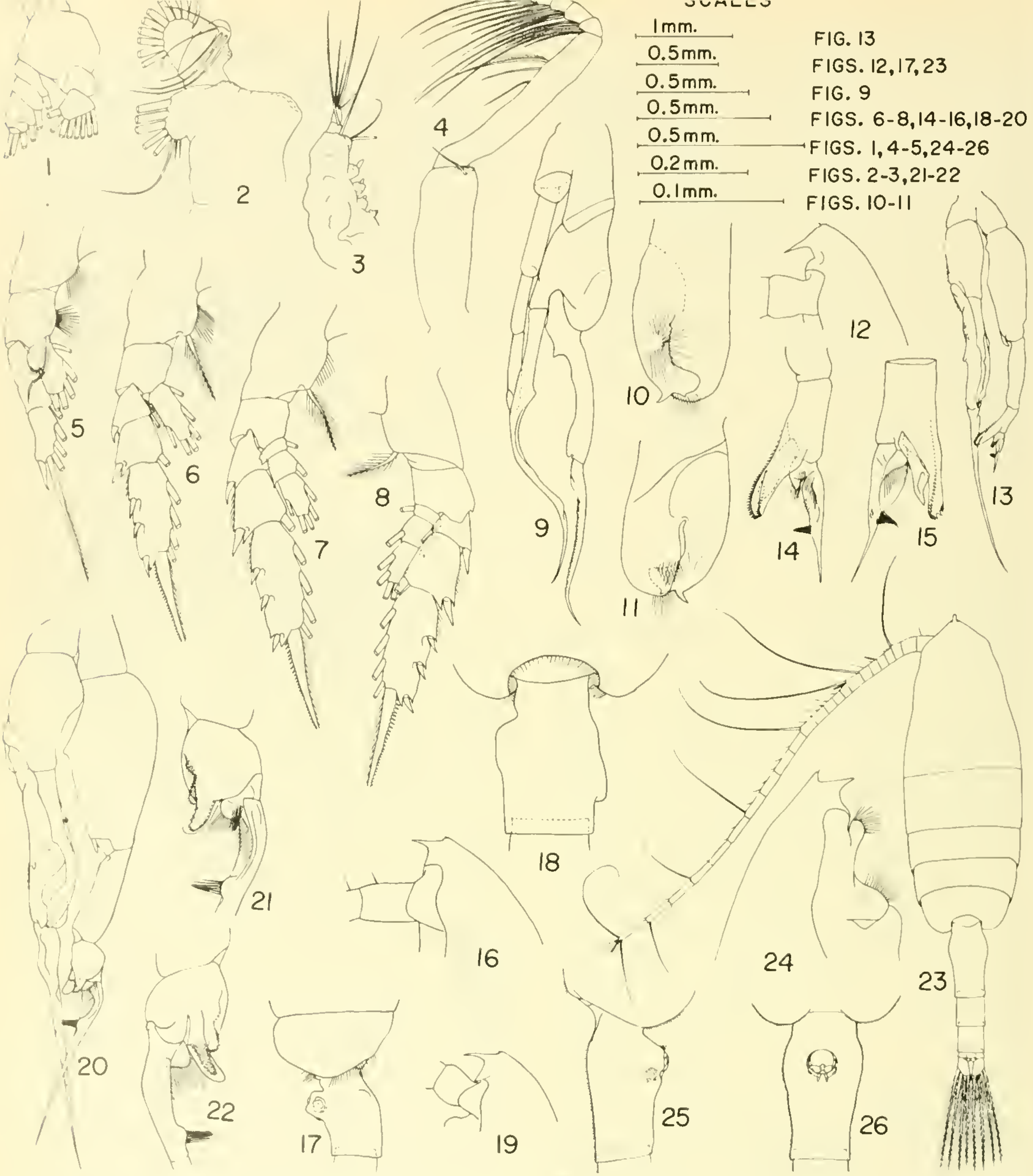
SCALES
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FIG. 13
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FIGS. 12, 17, 23
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FIG. 9
0.5mm.
FIGS. 6-8, 14-16, 18-20
0.5mm.
FIGS. 1, 4-5, 24-26
0.2mm.
FIGS. 2-3, 21-22
0.1mm.
FIGS. 10-11
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PLATE 7. Figs. 1–11, *Euchirella unispina*, new species. Male: fig. 1, mandibular palp; fig. 2, maxillule; fig. 3, maxilla; fig. 4, maxilliped; fig. 5, first leg; fig. 6, second leg; fig. 7, third leg; fig. 8, fourth leg; fig. 9, fifth pair of legs, posterior aspect; fig. 10, terminal part of left fifth leg, posterior aspect; fig. 11, *idem*, anterior aspect. Figs. 12–15, *Euchaeta spinosa*. Male: fig. 12, forehead, lateral view; fig. 13, fifth pair of legs, anterior aspect; fig. 14, distal part of left fifth leg, anterior aspect; fig. 15, *idem*, posterior aspect. Figs. 16–22, *Euchaeta media*. Female: fig. 16, forehead, lateral view; fig. 17, posterior part of metasome and genital segment, lateral view; fig. 18, *idem*, dorsal view. Male: fig. 19, forehead, lateral view; fig. 20, fifth pair of legs, anterior aspect; fig. 21, middle part of exopod of left fifth leg, anterior aspect; fig. 22, *idem*, posterior aspect. Figs. 23–26, *Euchaeta wrighti*, new species. Female: fig. 23, habitus, dorsal view; fig. 24, forehead, lateral view; fig. 25, genital segment, lateral view; fig. 26, *idem*, ventral view.

large and 2 small setae at the inner apex. The endopod and the exopod are small and 1-segmented, and have 5 and 11 setae, respectively.

The maxilla (plate 6, fig. 10) is short and has 5 prominent lobes. Each of the first to fourth lobes has a transverse row of small spinules on the posterior surface. The first lobe has in addition 3 long spinulose setae and 1 short, spinulose seta; the second and third lobes each have 2 long spinulose setae and one short spinulose seta; and each of the fourth and fifth lobes has one strong, dagger-shaped spine, 1 long spinulose seta, and 1 short spinulose seta. The endopod seems to be 4-segmented. Each of the first 3 segments has 1 spinulose seta. These setae are about equally long. The terminal segment has 3 short setae. In addition, the second and third segments each have a tiny seta.

The maxilliped (plate 6, fig. 11) has a slender basipod, and a short endopod that is about one-half the length of the basis. The coxa has four groups of setae, composed of 1, 2, 3, and 3 setae, respectively. Some scattered spinules are at the insertions of the setae of the last group. The basis has 3 setae at the middle and 2 setae at the distal end of the internal margin, in addition to a row of spinules along the proximal portion of the same margin. The endopod consists of 5 segments which have 4, 3, 3, 3 + 1, and 4 setae, respectively.

The first pair of legs (plate 6, fig. 12) has 2-segmented exopods and 1-segmented endopods. The basipod is fringed with hairs along the internal margin and has a seta at the distal end of the same margin. The endopod is slightly shorter than the first exopodal segment, and its external margin has a round tubercle that bears a transverse row of spinules on the anterior surface. The endopod has 3 internal setae and 2 apical setae. The first exopodal segment has 1 internal seta and 2 subequal external spines. The second exopodal segment has 1 strong external spine, 3 internal setae, and 1 long apical spine.

In the basipod of the second leg (plate 6, fig. 13), the coxa is fringed with hairs only along the internal margin and has an internal seta. The endopod is a single segment (a line of fusion is visible in stained specimens) that is slightly shorter than the combined length of the first and second exopodal segments. The endopod has 3 internal setae, 1 external seta, and 2 apical setae. The first and second exopodal segments each have 1 internal seta and 1 strong external spine. The third exopodal segment is longer than the first and second segments combined and has 3 strong external spines, 4 internal setae, and 1 long terminal spine that is armed with a row of acute teeth along the external margin.

The third leg (plate 6, fig. 14) is slightly larger than the second, but its basipod and exopod are similar in anatomical details to those of the second. The endopod is 3-segmented; the segments have 1, 1, and 5 setae, respectively. There are 2 triangular, flattened processes along the external margin of the first endopodal segment.

The fourth leg (plate 6, fig. 15) is slightly smaller than the third, and its coxa has a strong spine in addition to a stout internal seta. The spine extends beyond the distal end of the segment. Furthermore, the posterior surface of the coxa has 4 delicate setae, one of which is immediately distal to the insertion of the spine. Two such setae are also on the posterior surface of the basis. The exopod and endopod are anatomically similar to those of the third leg. The fifth pair of legs is absent.

Description of Male

The total length ranges from 3.84 to 4.03 mm. The proportional length of the prosome to the urosome is about 3.7:1. The prosome is more slender than in the female and has a low triangular forehead in dorsal aspect (plate 6, fig. 16). In lateral view the forehead is smoothly rounded into a strong rostrum and devoid of crests (plate 6, fig. 18). The cephalosome and the first metasomal segment, as well as the fourth and fifth metasomal segments, are completely fused, as they are in the female. The posterolateral margins of the metasome are rounded.

The urosome (plate 6, fig. 19) consists of 5 free segments and the caudal rami. The segments and the caudal rami have the following proportional lengths, from anterior to posterior: 25:24:17:19:6:9. The distal margins of the second to fourth urosomal segments are each fringed with a row of small spinules.

The 24-segmented antennule (plate 6, figs. 17 and 20) reaches the end of the second urosomal segment when applied against the body. Articulations between the 8th and 9th, the 11th and 12th, and the 23d and 24th segments are incomplete.

In the antenna (plate 6, fig. 21), the endopod is much better developed than in the female, reaching about two-thirds the length of the exopod. The basipod and the first endopodal segment, however, are devoid of setae.

The mouth parts are all reduced. The mandible (plate 7, fig. 1) lacks the mandibular blade. In the maxillule (plate 7, fig. 2), the first inner lobe is reduced to a mere round process that lacks setae or spines, and the second and third inner lobes are absent. The basis has no setae. The endopod is small, with 5 setae, but the exopod is much better developed than in the female and has 10 large setae plus 1 small seta.

In the maxilla (plate 7, fig. 3), the first to fourth lobes lack setae or spines. The fifth lobe has 2 setae. The endopod is 2-segmented and has 1 seta on the first and 4 setae on the second segment. In addition, there is a seta at the insertion of the endopod. The coxa of the maxilliped (plate 7, fig. 4) has a single seta and some scattered spinules on the distal lobe.

The legs of the male differ from those of the female in certain respects. In the first leg (plate 7, fig. 5), the first exopodal segment lacks external spines. The endopod of the second leg (plate 7, fig. 6) is a single segment without a visible line of fusion. The fourth leg (plate 7, fig. 8) lacks coxal spines and closely resembles the third (plate 7, fig. 7), but differs from the same leg of the female.

The fifth pair of legs (plate 7, fig. 9) consists of a uniramose left leg and a well-developed, biramose right leg. The left leg has 5 segments. The small distal segment is inserted a short distance proximal to the end of the preceding segment; the 2 segments together thus form a minute chela. The distal segment carries 2 teeth apically. The external tooth, which is the larger, curves outward, the internal one inward (plate 7, figs. 10 and 11). The right leg consists of a 2-segmented basipod, a 1-segmented endopod, and a 2-segmented exopod. The basipod is well developed, reaching the middle of the third segment of the left leg. The endopod is S-shaped, and has a triangular prominence along the external margin, one-third the length from the proximal end. The first exopodal segment has 2 prominences along the proximal one-third of the internal margin; the distal one of these is much larger than the other. The distal segment is S-shaped and has a row of small teeth along the internal margin.

Remarks

This species is closely related to *E. truncata*, but the female can easily be distinguished from that of the latter by her smaller size and the shape of the genital segment. The male of this species is characterized by the shapes of the teeth on the terminal segment of the left fifth leg and by the arrangement of the prominences on the exopod and endopod of the right fifth leg.

Type material of *E. unispina* from station 5 has been deposited in the U.S. National Museum as follows: Holotype female (USNM 113238); allotype male (USNM 113239); six females as paratypes (USNM 113240).

Euchirella amoena Giesbrecht, 1888

Occurrence

Sta. 3. 1 adult female, 3.84 mm.;
1 adult male, 3.20 mm.;
3 fifth copepodid females, 2.89 to 3.07 mm.;
4 fifth copepodid males, 3.00 to 3.09 mm.
Sta. 5. 2 adult females, 3.74 to 3.84 mm.;
3 adult males, 3.45 to 3.55 mm.;
2 fifth copepodid males, 3.26 mm.
Sta. 7. 1 fifth copepodid female, 3.13 mm.;
1 fifth copepodid male, 3.16 mm.
Sta. 9. 1 fifth copepodid female, 3.00 mm.

Remarks

The male of this species had been known as *E. amoena* and the female as *E. brevis*, until Grice (1962) synonymized them.

The female is well characterized by the stout, almost globose body, the last metasomal segment (with a pointed ridge on its posterolateral margin), and by the presence of 4 small acute teeth near the base of the internal seta of the coxa of the fourth leg.

The adult male can be recognized easily by the characteristic fifth pair of legs, which has a strong spine on the internal margin of the first segment of the right exopod. The fifth copepodid male is distinguished by the mandible, which, like that of the adult female, has a strong spine on the basis.

Euchirella rostrata Claus, 1866

Occurrence

Sta. 5. 12 adult females, 3.26 to 3.45 mm.
Sta. 7. 22 adult females, 3.36 to 3.64 mm.;
1 adult male, 2.97 mm.
Sta. 9. 17 adult females, 3.36 to 3.74 mm.;
1 adult male, 3.00 mm.
Sta. 13. 3 adult females, 3.60 to 3.80 mm.
Sta. 15. 6 adult females, 3.80 to 4.00 mm.

Remarks

This species is one of the most common in the present collections, but the male is rare.

Undeuchaeta plumosa Lubbock, 1856

Occurrence

Sta. 5. 4 adult females, 3.74 to 3.93 mm.
Sta. 9. 5 adult females, 3.84 to 4.12 mm.;
2 adult males, 3.55 to 3.72 mm.

Remarks

The present specimens are in full agreement with the figures given by Grice (1962).

FAMILY EUCHAETIDAE

Euchaeta marina (Prestandrea, 1833)

Occurrence

Sta. 3. 1 fifth copepodid female, 2.90 mm.;
3 adult males, 3.60 to 3.74 mm.
Sta. 5. 1 adult female, 3.55 mm.

Remarks

According to Grice (1962), this species is fairly common in the equatorial Pacific Ocean, but it seems to be rare in the central North Pacific.

Euchaeta spinosa Giesbrecht, 1892
(Plate 7, figs. 12–15)

Occurrence

Sta. 3. 5 adult females, 6.24 to 6.43 mm.;
1 adult male, 6.24 mm.
Sta. 5. 13 adult females, 6.33 to 6.91 mm.;
7 adult males, 5.97 to 6.24 mm.
Sta. 7. 3 adult females, 6.33 to 6.72 mm.;
1 adult male, 6.33 mm.
Sta. 9. 2 adult females, 6.33 mm.;
4 adult males, 6.14 to 6.52 mm.
Sta. 13. 3 adult females, 6.81 to 7.20 mm.

Remarks

The female of this species can easily be recognized by the high frontal prominence of the head, the slender rostrum, and the asymmetrical genital segment.

The male has a very slender body with a triangularly produced forehead (fig. 12). The right fifth leg (fig. 13) has a 2-segmented exopod and a 1-segmented endopod; the endopod is as long as the first segment of the exopod. The left fifth leg has a 3-segmented exopod and a small rudimental endopod. The second exopodal segment has distally a projection which is as long as the segment itself and which has a row of acute, triangular teeth along the margin (figs. 14 and 15).

Euchaeta media Giesbrecht, 1888
(Plate 7, figs. 16–22)

Occurrence

Sta. 5. 2 adult females, 4.03 to 4.12 mm.
Sta. 9. 11 adult females, 4.22 to 4.51 mm.;
5 adult males, 3.79 to 4.03 mm.
Sta. 13. 1 adult female, 4.51 mm.

The female (figs. 16–18) is well characterized by the shape of the genital segment, but the description of the male is rather incomplete (Wilson, 1950). The following description was made from the specimens from station 9.

Description of Male

The total length ranges from 3.79 to 4.03 mm. The proportional lengths of the prosome and urosome are 2.2:1. The forehead in dorsal aspect is produced triangularly, but in lateral view is smoothly rounded into a slender rostrum that is curved slightly downward (fig. 19). The antennule is 23-segmented and reaches to about the distal end of the metasome.

The right fifth leg (fig. 20) consists of a stout basipod, a 2-segmented exopod, and a 1-segmented endopod. The endopod is shaped like a ladle and is equal in length to the proximal exopodal segment. The second exopodal segment is like an elongated spine, enlarged at its base and acuminate at the tip. The left fifth leg has a much stouter basipod, a 3-segmented exopod, and a rudimental endopod. Three projections arise from the mediodistal corner of the second exopodal segment, and two of them have a row of teeth along the margin (figs. 21 and 22). The third exopodal segment is tapered distally into a slender spine; the proximal portion of the segment is hollow along the internal margin, which is fringed with long hairs; at the distal end of the hollow portion is a small knob, which has a few slender spines.

Remarks

Tanaka (1958) considered *Euchaeta acuta* var. *pacifica*, established solely on the male by Esterly (1911), synonymous with *E. media*. Esterly's description of the fifth pair of legs (the only structure described) however, seems too brief for a positive identification of the form.

Euchaeta pubera Sars, 1907

Occurrence

Sta. 5. 1 adult female, 3.84 mm.
Sta. 7. 3 adult females, 4.32 to 4.41 mm.

Remarks

The female is well characterized by the evenly rounded posterolateral corners of the metasome; the symmetrical genital segment, which in dorsal aspect is equally swollen on each side; and the hooklike process at the right side of the genital orifice. The posterior part of the body is covered with fine hairs.

Euchaeta wrighti, new species

(Plate 7, figs. 23–26; plate 8, figs. 1–3)

Occurrence

Sta. 3. 1 adult female, 2.73 mm.

Description of Female

The proportional lengths of the prosome and urosome are about 2:1. The general shape of the body is slender (plate 7, fig. 23). The cephalosome and the first metasomal segment, as well as the fourth and fifth metasomal segments, are fused, but a line of fusion between the cephalosome and the first metasomal segment is clearly visible after staining. The forehead in both dorsal and lateral view is produced into a process, which carries a sensory hair (plate 7, fig. 24). The rostrum is strong, pointing straight downward. The posterolateral margins of the metasome are smoothly rounded.

The urosome is 4-segmented; the segments, with the caudal rami, have the following proportional lengths, from anterior to posterior: 44:22:17:6:11.

The genital segment (plate 7, figs. 25 and 26) is long and slender. In dorsal aspect it is almost perfectly symmetrical—equally swollen on both sides. At about one-third the length from the proximal end it has a large genital swelling clearly visible in lateral aspect. The distal portion of the metasome and the whole urosome are densely covered with very fine hairs.

The antennule is 23-segmented, and, when fully extended, reaches as far as the end of the caudal ramus. The maxillule is best described by reference to plate 8, figure 1. In the maxilla, one of the 6 apical setae has long spines, in addition to short spinules that cover it entirely.

The basipod of the first leg (plate 8, fig. 2) is fringed with hairs along the internal margin and has the customary curved seta on the distal medial end of the basis. The exopod is 2-segmented. The external margin of the first segment is almost straight and has a fine spine near the distal end; the internal margin has a single seta. The second segment has a fine external spine, 3 internal setae, and 1 terminal spine, which is about four times as long as the segment. The endopod is a single segment; its external margin has a round tubercle armed with a row of fine spinules, the internal margin has 3 setae, and the apex 2 setae.

The coxa of the second leg (plate 8, fig. 3) has a row of hairs and a strong seta on the internal margin. The exopod is 3-segmented, with relatively small external spines. Of these spines the one on the second segment is the largest, but it does not reach as far as the base of the first external spine of the third segment. The terminal spine of the exopod is about as long as the third exopodal segment. The endopod is a single segment and is slightly shorter than the first 2 exopodal segments combined.

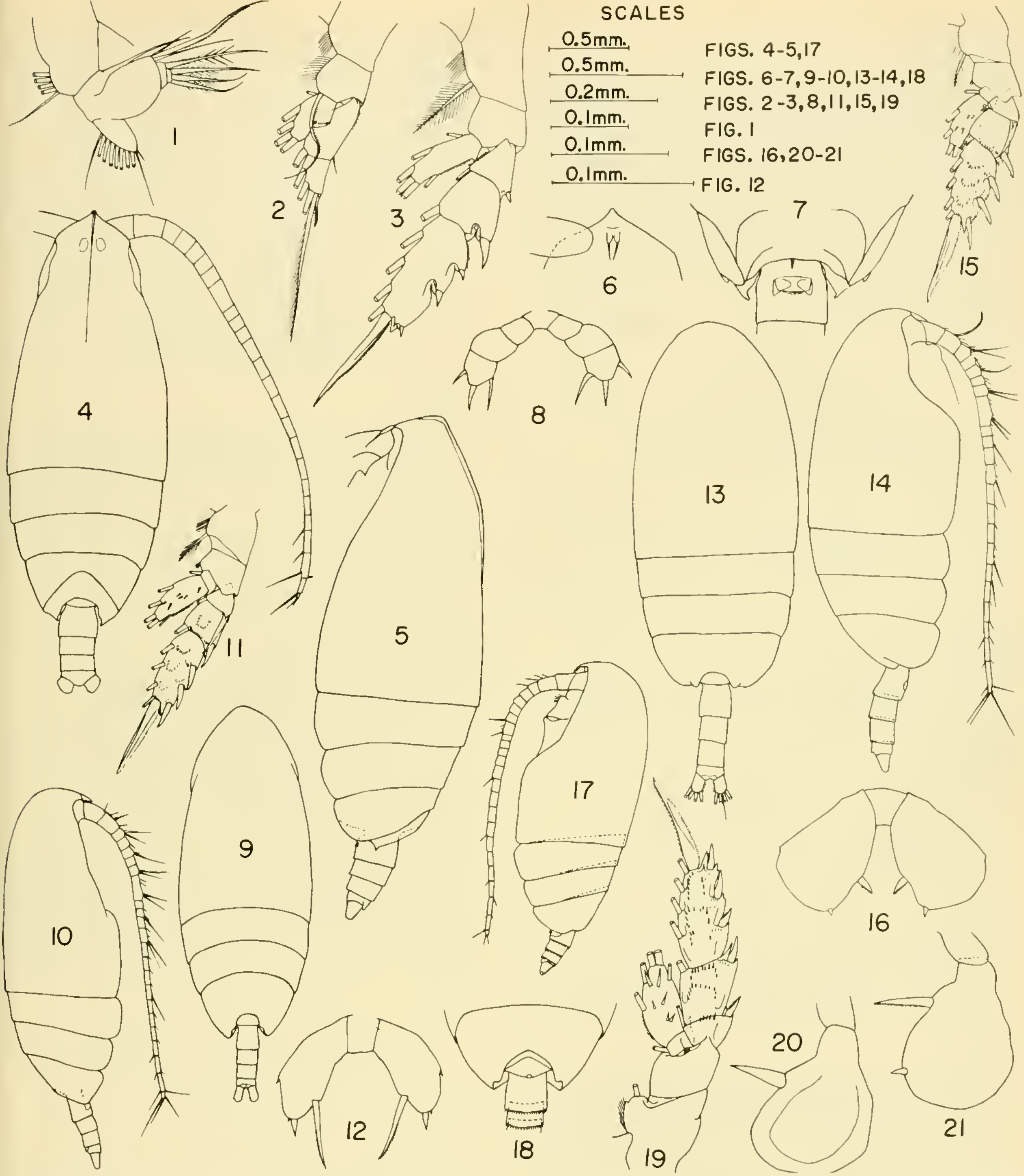
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PLATE 8, Figs. 1–3, *Euchaeta wrighti*, new species. Female: fig. 1, maxillule; fig. 2, first leg; fig. 3, second leg. Figs. 4–8, *Lophothrix latipes*. Female: fig. 4, habitus, dorsal view; fig. 5, habitus, lateral view; fig. 6, forehead, ventral view; fig. 7, posterior part of metasome and genital segment, ventral view; fig. 8, fifth pair of legs. Figs. 9–12, *Scolecithricella minor*. Female: fig. 9, habitus, dorsal view; fig. 10, habitus, lateral view; fig. 11, second leg; fig. 12, fifth pair of legs. Figs. 13–16, *Scolecithricella dentata*. Female: fig. 13, habitus, dorsal view; fig. 14, habitus, lateral view; fig. 15, second leg; fig. 16, fifth pair of legs. Figs. 17–21, *Scolecithricella ovata*. Female: fig. 17, habitus, lateral view; fig. 18, posterior part of metasome and anterior part of urosome, dorsal view; fig. 19, second leg; fig. 20, left fifth leg; fig. 21, right fifth leg.

Remarks

Although only a single specimen was found, I believe that its characters are sufficiently distinct to consider it as a member of a valid species. The present specimen, in general shape of the body, appears to be related to *E. plana* Mori, 1937, redescribed by Tanaka (1958). The obvious difference in the location of the genital swelling, however, prevents it from being referred to that species.

The only specimen was accidentally destroyed.

FAMILY PHAENNIDAE

Phaenna spinifera Claus, 1863

Occurrence

Sta. 3. 10 adult females, 1.84 to 2.11 mm.;
1 adult male, 1.94 mm.
Sta. 5. 5 adult females, 1.91 to 2.40 mm.
Sta. 7. 5 adult females, 2.02 to 2.11 mm.

Remarks

This species can readily be recognized by the nearly rounded body in dorsal aspect. In details the present specimens are in full agreement with the figures given by Giesbrecht (1892).

FAMILY SCOLECITHRICIDAE

Lophothrix latipes (T. Scott, 1894)
(Plate 8, figs. 4–8)

Occurrence

Sta. 3. 1 adult female, 3.06 mm.
Sta. 5. 9 adult females, 3.03 to 3.16 mm.
Sta. 7. 1 adult female, 3.23 mm.

Remarks

This species can be recognized by the following characters: The head has a long, low crest and two large ocular lenticels that are clearly visible in stained specimens (figs. 4 and 5). The rostrum consists of a thickened, incised basal portion, which has two fine rostral filaments (fig. 6). The posterolateral corner of the metasome (fig. 7) is produced into a point, the tip of which in dorsal or ventral view curves inward and reaches to about the middle of the genital segment. The fifth leg (fig. 8) is uniramous and 4-segmented; it is considerably dilated toward the distal end and has 3 spines on the apex. The inner spine is the longest.

Scolecithrix danae (Lubbock, 1856)

Occurrence

Sta. 3. 3 fifth copepodid females, 1.50 to 1.55 mm.;
2 adult males, 2.07 to 2.10 mm.
Sta. 5. 8 adult females, 2.01 to 2.17 mm.;
6 adult males, 2.11 to 2.17 mm.
Sta. 7. 4 adult females, 2.14 to 2.17 mm.;
1 adult male, 2.11 mm.

Remarks

The female of this species can readily be distinguished by her very robust body and by the genital segment, which has a ventral projection in the form of a shovel. Giesbrecht (1892) and Rose (1942) have described and figured this species in detail.

Scolecithrix bradyi Giesbrecht, 1888

Occurrence

Sta. 3. 1 adult female, 1.22 mm.
Sta. 5. 2 adult females, 1.32 mm.;
1 adult male, 1.51 mm.
Sta. 7. 5 adult females, 1.32 to 1.38 mm.
Sta. 9. 1 adult female, 1.40 mm.

Remarks

The asymmetrical last metasomal segment and the extremely short urosome identify the female of this species and the structure of the fifth pair of legs identifies the male. Figures of these characters have been given by Grice (1962).

Scolecithricella minor (Brady, 1883)
(Plate 8, figs. 9–12)

Occurrence

Sta. 16. 1 adult female, 1.42 mm.

Remarks

The urosome of the female has a characteristic shape; it is markedly narrow as compared with its robust prosome (figs. 9 and 10). The posterolateral margin of the metasome in lateral view is triangularly produced into a blunt tip, which reaches the middle of the genital segment. The first exopodal segment of the second leg (fig. 11) has a long external spine that extends beyond the distal margin of the second exopodal segment. The fifth leg (fig. 12) consists of a basal portion, common to both legs, and a plate-shaped apical segment, which has a long internal spine, a short, strong apical spine, and a small external spine. An additional small spine is located immediately lateral to the apical spine.

Scolecithricella dentata (Giesbrecht, 1892)
(Plate 8, figs. 13–16)

Occurrence

Sta. 5. 1 adult female, 1.48 mm.
Sta. 15. 1 adult female, 1.55 mm.
Sta. 16. 1 adult female, 1.68 mm.

Remarks

The following characters mainly serve to identify the female of this species: The prosome is nearly elliptical in dorsal aspect (fig. 13); its posterolateral margin in lateral aspect (fig. 14) has a distinct incision that is also clearly visible in dorsal view. The external spine of the first exopodal segment of the second leg (fig. 15) is long, slightly curved inward, and reaches the distal margin of the second exopodal segment. On the third exopodal segment of the same leg, 3 small teeth lie along the external margin immediately proximal to each of the second and third external spines. The fifth leg (fig. 16) is laminate and almost rectangular; it has a tiny spine at the tip and a larger spine on the internal margin.

Scolecithricella ovata (Farran, 1905)
(Plate 8, figs. 17–21)

Occurrence

Sta. 5. 1 adult female, 1.98 mm.
Sta. 7. 1 adult female, 1.88 mm.

Remarks

The female of this species can easily be distinguished by the posterolateral margin of the metasome, which has a distinct notch visible in either lateral or dorsal view (figs. 17 and 18), and by the second and fifth pairs of legs. The coxa of the second leg (fig. 19) has a distinct notch on the external margin; the roundly produced internal margin also has a distinct notch, in addition to a row of hairs and a seta. The fifth leg (fig. 20) is shaped like a paddle with a cylindrical "handle" by which it is attached to a common basal portion. The internal margin of the paddle-shaped portion has a well-developed spine. One specimen had a small second internal spine close to the distal end of the right leg (fig. 21).

Scolecithricella vittata (Giesbrecht, 1892)

Occurrence

Sta. 5. 2 adult females, 1.74 to 1.80 mm.

Remarks

The female is readily recognized by the characteristic fifth pair of legs. Figures of this and other characters have been given by Grice (1962).

Scolecithricella auropecten (Giesbrecht, 1892)
(Plate 9, figs. 1–4)

Occurrence

Sta. 5. 9 adult females, 2.17 to 2.37 mm.
Sta. 7. 6 adult females, 2.11 to 2.34 mm.
Sta. 13. 1 adult female, 2.40 mm.

Remarks

The female of this species can be identified easily by the posterolateral margin of the metasome, which in lateral view has a round depression (fig. 1), and by the fifth pair of legs (fig. 2). Figures of the mouth parts and the swimming legs have been given by Rose (1942) and Giesbrecht (1892).

Two specimens possessed abnormal fifth pairs of legs (figs. 3 and 4) but appeared to be identical with the normal specimens in all other details.

FAMILY METRIDIIDAE

Metridia lucens Boeck, 1865

Occurrence

Sta. 16. 2 adult females, 2.68 to 2.78 mm.;
9 fifth copepodid females, 1.90 to 2.07 mm.;
4 fifth copepodid males, 1.73 to 1.84 mm.

Remarks

This species is easily recognized by two characters. The posterolateral margin of the met-

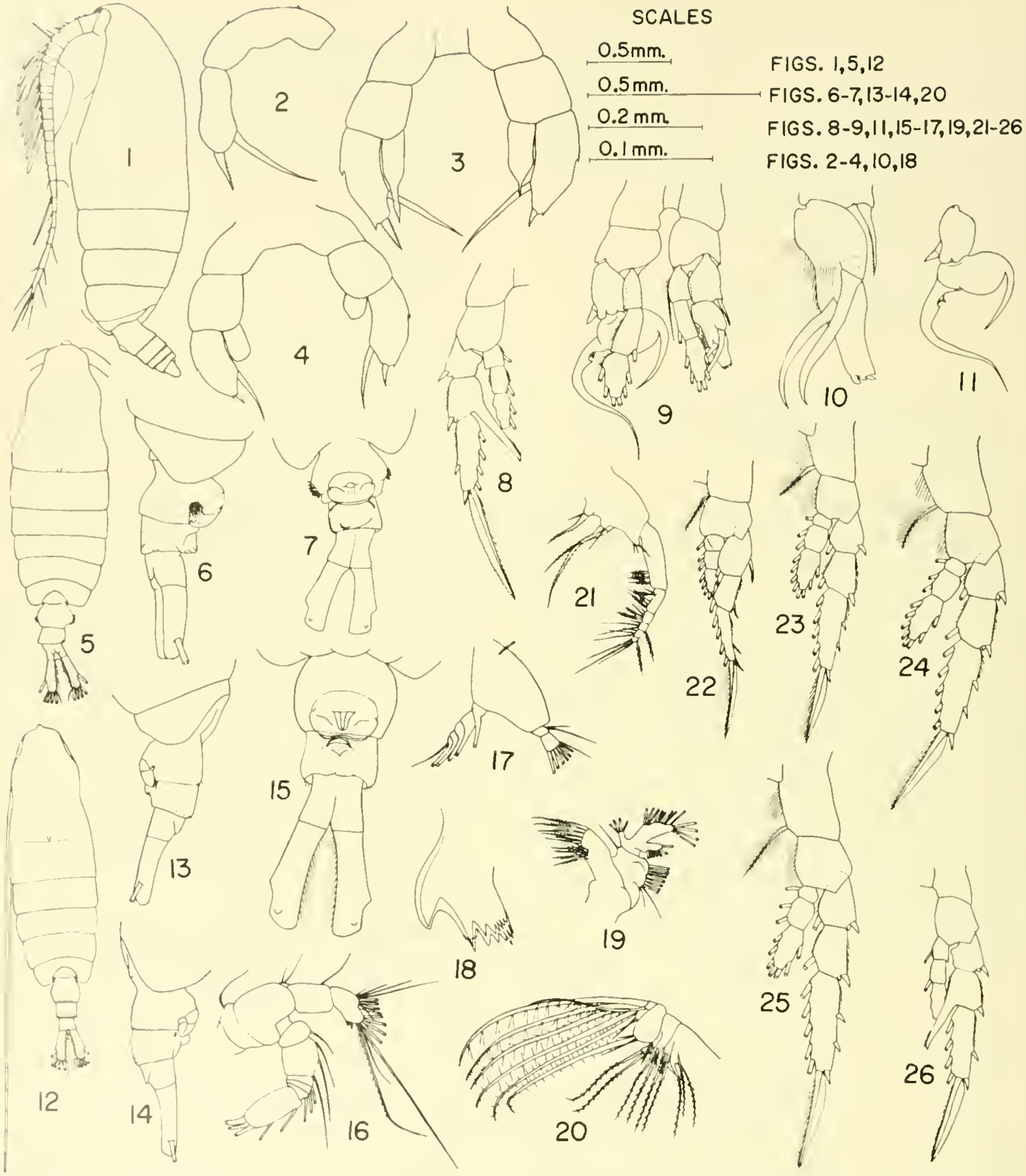
SCALES
0.5 mm. FIGS. 1,5,12
0.5 mm. FIGS. 6-7,13-14,20
0.2 mm. FIGS. 8-9,11,15-17,19,21-26
0.1 mm. FIGS. 2-4,10,18
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PLATE 9. Figs. 1-4, *Scolecithricella auropecten.* Female: fig. 1, habitus, lateral view; fig. 2, fifth leg; figs. 3-4, abnormal fifth pairs of legs. Figs. 5-11, *Centropages violaceus.* Female: fig. 5, habitus, dorsal view; fig. 6, posterior part of metasome and urosome, lateral view; fig. 7, *idem*, ventral view; fig. 8, fifth leg. Male: fig. 9, fifth pair of legs, anterior aspect; fig. 10, distal part of exopod of left fifth leg; fig. 11, exopod of right fifth leg. Figs. 12-26, *Centropages elegans.* Female: fig. 12, habitus, dorsal view; fig. 13, posterior part of metasome and urosome, viewed from left side; fig. 14, *idem*, viewed from right side; fig. 15, *idem*, ventral view; fig. 16, antenna; fig. 17, mandibular palp; fig. 18, cutting edge of manducatory plate; fig. 19, maxillule; fig. 20, maxilla; fig. 21, maxilliped; fig. 22, first leg; fig. 23, second leg; fig. 24, third leg; fig. 25, fourth leg; fig. 26, fifth leg.

asome is produced into a point. In the second leg, the basis has a hook on the distal margin and the internal margin of the first endopodal segment is proximally provided with a deep invagination guarded by 3 strong teeth.

Brodsky (1950) distinguished the Pacific form of *Metridia lucens* from the Atlantic form and gave it a new name, *Metridia pacifica*. Damkaer (1964 and personal communication) examined specimens from both the Pacific and the Atlantic and found no morphological differences to warrant two species.

FAMILY CENTROPAGIDAE

Centropages bradyi Wheeler, 1900

Occurrence

Sta. 5. 1 adult female, 1.95 mm.
Sta. 9. 1 adult male, 1.74 mm.
Sta. 13. 30 adult females, 1.91 to 2.08 mm.; 8 adult males, 1.78 to 1.91 mm.
Sta. 15. 11 adult females, 2.00 to 2.24 mm.; 2 adult males, 1.97 to 2.00 mm.

Remarks

This species is characterized by the rounded posterolateral corners of the metasome, the symmetrical genital segment, and the large caudal rami, each of which has a fingerlike projection between the two lateral terminal setae.

Centropages elongatus Giesbrecht, 1896

Occurrence

Sta. 3. 7 adult females, 1.74 to 1.90 mm.; 7 adult males, 1.65 to 1.80 mm.
Sta. 5. 1 adult female, 1.91 mm.
Sta. 7. 1 adult female, 1.91 mm.; 1 adult male, 1.81 mm.

Remarks

The present specimens are in agreement with the figures given by Grice (1962).

Centropages violaceus (Claus, 1863)
(Plate 9, figs. 5–11)

Occurrence

Sta. 3. 1 adult female, 2.17 mm.; 4 adult males, 2.04 to 2.11 mm.
Sta. 5. 3 adult females, 2.11 to 2.14 mm.; 4 adult males, 2.04 to 2.17 mm.
Sta. 7. 11 adult females, 2.14 to 2.24 mm.; 2 adult males, 2.14 to 2.17 mm.

Remarks

The female of this species can be distinguished by the genital segment, which in dorsal aspect (fig. 5) is slightly asymmetrical—the right side is slightly more swollen. The swellings of both the right and left sides have a group of spinules (figs. 6 and 7). The second urosomal segment ventrally lacks the knoblike projection shown in the figure by Giesbrecht (1892). In the fifth leg (fig. 8) the spiniform projection of the second exopodal segment is slightly shorter than the third exopodal segment and has a row of stiff hairs along the internal distal margin.

The male of this species can be identified by the fifth pair of legs (figs. 9–11). The second exopodal segment of the right leg is nearly elliptical; the spinous projection of the segment bends sharply outward. The terminal claw has a deep notch at the proximal portion of the internal margin; in this notch is an acute tooth.

Centropages elegans Giesbrecht, 1895
(Plate 9, figs. 12–26; plate 10, figs. 1–6)

Centropages elegans Giesbrecht, 1895, p. 256, plate 4, figs. 1–2.

Occurrence

Sta. 3. 21 adult females, 1.86 to 2.04 mm.; 10 adult males, 1.84 to 1.97 mm.
Sta. 5. 16 adult females, 1.94 to 2.14 mm.; 9 adult males, 1.84 to 2.01 mm.
Sta. 7. 3 adult females, 2.01 to 2.07 mm.; 4 adult males, 1.94 to 2.04 mm.

Description of Female

The total length of the specimens ranges from 1.86 to 2.14 mm. The prosome is about three times as long as the urosome. The cephalosome in dorsal aspect has a small semicircular projection at the tip and a knoblike process at the posterodorsal margin (plate 9, fig. 12). The first metasomal segment is incompletely separated from the cephalosome—a line of joint is visible only on the dorsal region. The posterolateral margins of the metasome are smoothly rounded.

The urosome (plate 9, figs. 13–15) is 3-segmented; the segments and the caudal rami have

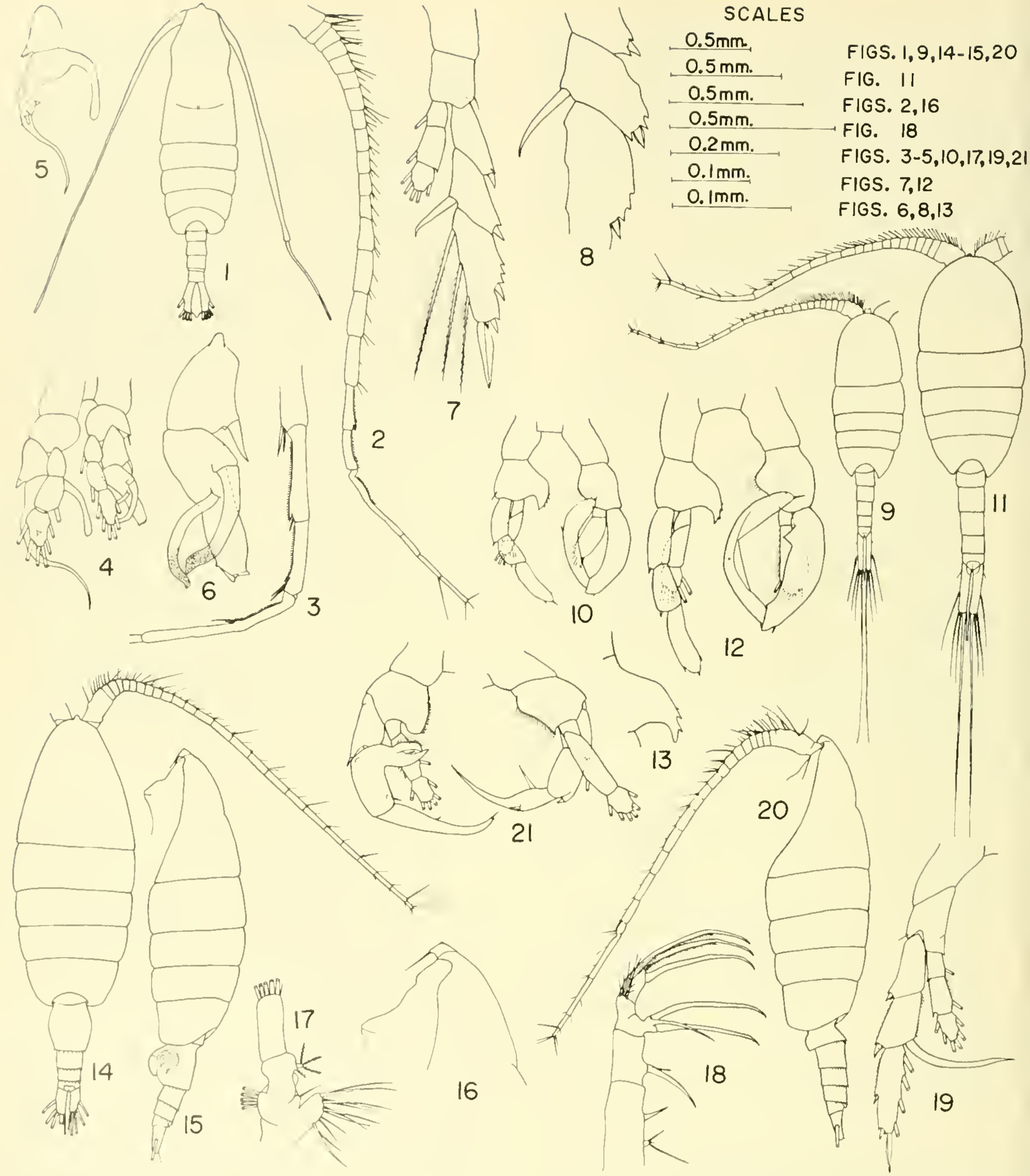
SCALES
0.5mm. FIGS. 1,9,14-15,20
0.5 mm. FIG. 11
0.5mm. FIGS. 2,16
0.5mm. FIG. 18
0.2mm. FIGS. 3-5,10,17,19,21
0.1mm. FIGS. 7,12
0.1mm. FIGS. 6,8,13
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PLATE 10. Figs. 1–6, *Centropages elegans.* Male: fig. 1, habitus, dorsal view; fig. 2, right antennule; fig. 3, geniculated region of right antennule; fig. 4, fifth pair of legs, anterior aspect; fig. 5, exopod of right fifth leg; fig. 6, exopod of left fifth leg. Figs. 7–13, *Lucicutia flavicornis.* Female: fig. 7, fifth leg; fig. 8, abnormal exopod of left fifth leg. Male: fig. 9, habitus, dorsal view; fig. 10, fifth pair of legs, posterior aspect. Figs. 11–13, male abnormal in fifth pair of legs: fig. 11, habitus, dorsal view; fig. 12, fifth pair of legs, posterior aspect; fig. 13, inner projection of basis of left fifth leg. Figs. 14–21, *Heterorhabdus papilliger.* Female: fig. 14, habitus, dorsal view; fig. 15, habitus, lateral view; fig. 16, forehead, lateral view; fig. 17, maxillule; fig. 18, maxilla; fig. 19, fifth leg. Male: fig. 20, habitus, lateral view; fig. 21, fifth pair of legs, anterior aspect.

the following proportional lengths, from anterior to posterior: 28:20:16:36.

The genital segment is symmetrical, wider than long, and has dorsally a row of small spinules along its distal margin. The second urosomal segment has ventrally a knoblike projection and dorsally 2 rows of small spinules along the distal border. The caudal rami are symmetrical and about 3.5 times as long as wide.

The antennule is 24-segmented; the last 5 segments extend beyond the end of the caudal ramus. The endopod of the antenna (plate 9, fig. 16) is short—about one-half the length of the exopod. The second endopodal segment has 8 + 1 setae on the internal lobe and 6 + 1 setae on the external lobe.

The mandibular palp (plate 9, fig. 17) has a triangular basis, which has a seta on the posterior surface. The exopod is 5-segmented; each of the first to fourth segments has 1 seta, and the terminal segment 2 setae. The endopod is small; the first segment has 2 setae, and the second segment 7 setae. The mandibular blade (plate 9, fig. 18) consists of a large separate tooth and a plate with about 7 acute teeth.

The maxillule is relatively small; details of its structure are shown in plate 9, figure 19.

The maxilla (plate 9, fig. 20) is well developed. The first to fourth lobes each bear 2 +1 spinose setae. The fifth lobe is much better developed; it has 1 long spinose seta and 2 small spiniform setae. The endopod has 5 long spinose setae, 1 short spinose seta, and a small spiniform seta.

The coxa of the maxilliped (plate 9, fig. 21) is stout and has 3 well-developed lobes. The first lobe has 1 spinose seta plus 1 spiniform seta, the second lobe 2 spinose setae plus 1 spiniform seta, and the third lobe 3 small spiniform setae. The basis is about as long as the coxa and carries 3 setae distally. The endopod is also as long as the coxa and is 5-segmented.

The basipod of the first leg (plate 9, fig. 22) is stout and has an internal seta on each segment. The endopod is 3-segmented and shorter than the first and second exopodal segments combined. The first segment has 1 internal seta; the second segment, 2 internal setae; and the third segment, 3 internal setae, 1 external seta, and 2 terminal setae. The exopod is also 3-segmented; it has 1 + 1 + 2 external spines, 1 + 1 + 4 internal setae, and 1 terminal spine.

The second and third pairs of legs (plate 9, figs. 23 and 24) are similar. On the basipod, only the coxa has an internal seta. The endopod is 3-segmented and extends slightly beyond the distal border of the second exopodal segment. The segments have 1, 2, and 8 setae, respectively. The exopod is also 3-segmented; the first and second segments each have 1 external spine and 1 internal seta. The third segment has 3 external spines, 5 internal setae, and 1 terminal spine.

The fourth leg (plate 9, fig. 25) differs from the third leg only in the number of setae on the third endopodal segment—it has 7 setae instead of 8.

The basipod of the fifth leg has no setae (plate 9, fig. 26). The exopod is 3-segmented. The first segment has 1 external spine and a round projection along the internal margin. The second segment has 1 external spine and a strong spiniform projection from the internal margin. This projection is shorter than the third exopodal segment and has distally a row of stiff hairs along the internal margin. The third exopodal segment has 2 external spines, 4 internal setae, and a terminal spine. The endopod is also 3-segmented; it has 1 seta on the first segment, 1 on the second, and 6 on the third.

Description of Male

The total length ranges from 1.84 to 2.04 mm. The proportional lengths of the prosome and urosome are 2.8:1. The first metasomal segment is incompletely separated from the cephalosome; a line of separation is visible only on the dorsal side. The posterolateral corners of the metasome are smoothly rounded (plate 10, fig. 1). The urosome is 5-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 15:17:17:5:14:32. The caudal rami are about 3 times as long as wide.

The left antennule is 24-segmented; the last 2 segments extend beyond the end of the caudal ramus. The right antennule (plate 10, figs. 2 and 3) is modified for grasping the female. The external margins of the 17th to 19th segments are each fringed with a row of acute teeth.

The 18th and 19th segments are articulated by a "knee joint."

The antenna, the mouth parts, and the first to fourth pairs of legs are similar to those of the female.

The fifth pair of legs (plate 10, figs. 4–6) is asymmetrical—the right exopod is modified into a grasping organ in the form of a powerful chela. The left exopod is 2-segmented; the distal segment has two strong, curved spines, the distal parts of which are densely pitted.

Remarks

This species was established by Giesbrecht (1895) upon a single male specimen from the northeastern Pacific. As the species does not appear in any other lists, the present specimens constitute the first record since the original discovery. The female is described here for the first time. Sixteen female specimens have been deposited in the U.S. National Museum (USNM 113375, 113376).

FAMILY LUCICUTIIDAE

Lucicutia flavicornis (Claus, 1863)
(Plate 10, figs. 7–13)

Occurrence

Sta. 3. 2 adult females, 1.41 to 1.43 mm.
Sta. 5. 12 adult females, 1.38 to 1.94 mm.; 6 adult males, 1.45 to 1.48 mm.
Sta. 7. 1 adult male, 1.51 mm.
Sta. 15. 3 adult females, 1.65 to 1.94 mm.
Sta. 16. 1 adult female, 2.04 mm. 1 adult male, 1.66 mm.

Remarks

The female of this species can be distinguished by the elliptical prosome and the shape of the fifth pair of legs (fig. 7). The female from station 16 had an abnormal left fifth leg —2 teeth were present proximal to the external spine of the second exopodal segment (fig. 8).

The body of the male (fig. 9) is shaped like that of the female. The left antennule is 21-segmented and slightly modified for grasping the female. The basis of the left fifth leg (fig. 10) has internally a large projection pointed distally. The internal edge of this projection has 5 or 6 teeth. In the right fifth leg, both the exopod and the endopod are 2-segmented. The proximal exopodal segment is slightly curved inward and lacks processes on the internal margin.

Four male specimens abnormal in the shape of the fifth pair of legs were from stations 5 and 7. The general shape of the body of these males (fig. 11) does not differ from that of the normal male, but the fifth pair of legs (figs. 12 and 13) differs in the following aspects: The projection on the internal margin of the basis in the left leg is tapered distally, with 3 to 4 acute teeth along the internal edge. The first exopodal segment of the right leg has proximally a triangular process along the internal margin. The second exopodal segment of the same leg is pronouncedly curved.

FAMILY HETERORHABDIDAE

Heterorhabdus papilliger (Claus, 1863)
(Plate 10, figs. 14–21)

Occurrence

Sta. 5. 15 adult females, 1.88 to 2.24 mm.; 14 adult males, 1.98 to 2.07 mm.
Sta. 7. 15 adult females, 1.91 to 2.31 mm.; 6 adult males, 1.94 to 2.14 mm.
Sta. 9. 4 adult females, 2.17 to 2.21 mm.; 2 adult males, 2.14 to 2.17 mm.
Sta. 13. 4 adult females, 2.41 to 2.54 mm.; 12 adult males, 2.27 to 2.65 mm.
Sta. 15. 11 adult females, 2.40 to 2.62 mm.; 4 adult males, 2.55 to 2.62 mm.
Sta. 16. 18 adult females, 2.48 to 2.58 mm.; 10 adult males, 2.48 to 2.55 mm.

Remarks

This species is one of the most common in the present collections. It can be identified readily by the triangularly produced forehead in lateral aspect (figs. 16 and 20) and the 3 equal terminal spines of the maxilla (fig. 18). In the fifth leg of the female (fig. 19), the second exopodal segment has internally a long, curved spine, which is longer than the third exopodal segment. The fifth pair of legs (fig. 21) of the male has a beaklike projection on the internal margin of the second right exopodal segment.

Heterorhabdus abyssalis (Giesbrecht, 1889)
(Plate 11, figs. 1–6)

Occurrence

Sta. 9. 3 adult females, 2.47 to 2.69 mm.; 1 adult male, 2.41 mm.

Remarks

This species is recognized by the rounded forehead in lateral aspect (fig. 2) and the structure of the maxilla (fig. 4), the distal lobe of which has 2 spines of equal length and 1 slightly shorter spine. In the fifth pair of legs of the female (fig. 3), the internal spine of the second exopodal segment is about as long as the third exopodal segment and is fringed with fine hairs along the upper margin. The fifth pair of legs in the male (figs. 5 and 6) is characterized by the laminar protrusion on the internal margin of the right basis and the conical internal projection of the second segment of the right exopod.

Heterostylites longicornis (Giesbrecht, 1889)

Occurrence

Sta. 5. 2 adult females, 2.80 to 2.83 mm.; 1 adult male, 2.90 mm.
Sta. 7. 1 adult female, 2.90 mm.

Remarks

This species is closely similar to the species of *Heterorhabdus* but can easily be distinguished from the latter by the longer antennule, the armament of the mandibular blade, and the better developed endopod of the maxilla. In the female, the second exopodal segment of the fifth leg has a compound spine, with 6 to 7 points, medial to the regular external spine.

H. longicornis is distinguished from *H. major* only by its smaller size; there are practically no anatomical differences. The female of *H. longicornis*, according to Giesbrecht and Schmeil (1898), measures about 3.0 mm., but that of *H. major* measures about 5.0 mm.

FAMILY AUGAPTILIDAE

Haloptilus longicornis (Claus, 1863)

Occurrence

Sta. 3. 136 adult females, 2.00 to 2.24 mm.
Sta. 5. 44 adult females, 2.17 to 2.44 mm.
Sta. 7. 3 adult females, 2.14 to 2.34 mm.

Remarks

This species was one of the most common at the southern stations, but not a single male was found. The female can be recognized by the knoblike projection on the forehead, when viewed from above, and the very long antennule.

Haloptilus fertilis (Giesbrecht, 1892)
(Plate 11, figs. 7–20)

Occurrence

Sta. 3. 2 adult males, 2.89 to 3.16 mm.
Sta. 5. 3 adult males, 2.93 to 3.13 mm.

This species was erected on the basis of a male from the Mediterranean Sea (Giesbrecht, 1892). Grice (1962) obtained a single male from equatorial waters of the Pacific. The following description is based on the five adult males in the present collections.

Description of Males

The total length ranges from 2.89 to 3.16 mm. The proportional lengths of the prosome and urosome are about 5.6:1. The first metasomal segment is separated from the cephalosome, but the fourth and fifth metasomal segments are fused. The cephalosome in dorsal aspect has a broadly triangular forehead, and the oral region is more or less dilated. The posterolateral margins of the metasome are smoothly rounded (fig. 7).

The urosome (fig. 8) is 5-segmented. The first segment is nearly as long as the combined lengths of the succeeding 3 segments. The figure by Giesbrecht (1892, plate 42, fig. 5), however, shows the second to fourth urosomal segments relatively longer than those of the present specimens.

The right antennule is normal, 25-segmented, and reaches as far as the end of the caudal ramus. The 23-segmented left antennule (fig. 9) is modified for grasping the female. Each of the 14th to 16th segments has a swollen outer margin, and each of the 17th to 19th segments has a serrated lamella along the same margin. A knee joint is found between the 18th and 19th segments.

In the antenna (fig. 10), the exopod is only about one-third the length of the endopod. The

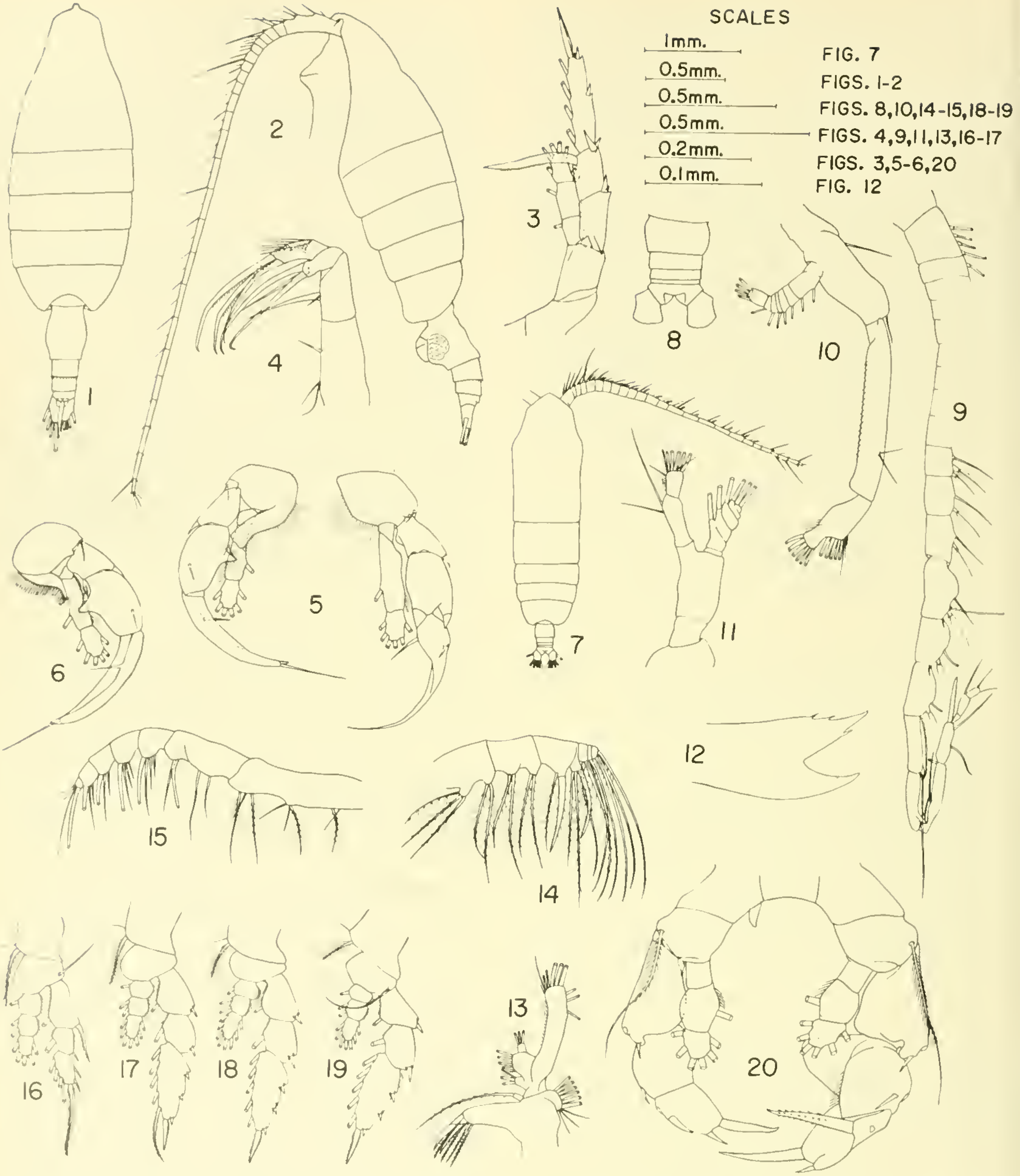
SCALES
1mm. FIG. 7
0.5mm. FIGS. 1-2
0.5mm. FIGS. 8,10,14-15,18-19
0.5mm. FIGS. 4,9,11,13,16-17
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PLATE 11. Figs. 1–6, *Heterorhabdus abyssalis*. Female: fig. 1, habitus, dorsal view; fig. 2, habitus, lateral view; fig. 3, fifth leg. Male: fig. 4, maxilla; fig. 5, fifth pair of legs, anterior aspect; fig. 6, right fifth leg, posterior aspect. Figs. 7–20, *Haloptilus fertilis*. Male: fig. 7, habitus, dorsal view; fig. 8, urosome, dorsal view; fig. 9, left antennule; fig. 10, antenna; fig. 11, mandibular palp; fig. 12, mandibular blade; fig. 13, maxillule; fig. 14, maxilla; fig. 15, maxilliped; fig. 16, first leg; fig. 17, second leg; fig. 18, third leg; fig. 19, fourth leg; fig. 20, fifth pair of legs posterior aspect.

exopod is 8-segmented, and the endopod 2-segmented. The first segment of the endopod is about 2.5 times as long as the second.

The mandibular palp (fig. 11) is slender and lacks setae on the basis. The endopod is slightly longer than the exopod. The cutting edge (fig. 12) of the mandibular blade consists of 2 strong rostral teeth, the inner of which has 2 small acute teeth along the internal margin and another along the external margin.

In the maxillule (fig. 13), the first inner lobe and the exopod are elongate. The first inner lobe has distally 7 spiniform setae, 2 of which are notably strong. The second and third inner lobes are small, and have 1 and 3 setae, respectively.

The maxilla (fig. 14) bears 6 well-developed lobes. The first lobe has 3 setae, each of the second to fourth lobes 2 setae, the fifth lobe 1 seta plus 1 strong spine, and the sixth lobe 2 setae plus 1 strong spine. The spine of the sixth lobe is slightly smaller than that of the fifth lobe. The endopod is 3-segmented and has 7 setae.

The coxa of the maxilliped (fig. 15) has 3 lobes, which have 2, 3, and 3 setae, respectively. The basis has 2 lobes, each with 2 setae. The endopod is 5-segmented; the first and second segments each have 4 setae, the third and fourth have 3, and the fifth has 4.

The basipod of the first leg (fig. 16) has 1 internal seta on the coxa and 1 external seta on the basis. Both the exopod and the endopod are 3-segmented. The first and second exopodal segments each have 1 internal seta and 1 external spine. The external spine of the first segment is notably long, extending beyond the end of the spine on the second segment. The third exopodal segment has 2 external spines, 4 internal setae, and 1 terminal spine. The endopod is about as long as the first 2 exopodal segments combined and has 1 seta on the first segment, 2 on the second, and 5 on the third.

The second to fourth pairs of legs (figs. 17–19) are similar. The coxa has 1 internal seta. The basis is naked in the second and third legs but has an external seta in the fourth leg. The exopod is 3-segmented; the first and second segments each have 1 external spine and 1 internal seta; and the third segment has 3 external spines, 5 internal setae, and 1 terminal spine. The endopod is also 3-segmented. The first segment bears 1 seta, and the second segment 2 setae. The third segments of the second and fourth legs have 7 setae, but that of the third leg has 8 setae.

The fifth pair of legs (fig. 20) is asymmetrical. The coxa of the left leg has a strong tooth on the internal margin. The basis in both the right and the left legs has a long plumose external seta. The second exopodal segment of the right leg has a large, conical protrusion on the internal margin. The right and left third exopodal segments both have 2 external spines and 1 large terminal spine; the first external spine of the right third exopodal segment is spinose and as long as the terminal spine. The endopods of both legs are 3-segmented; the first segment lacks setae, but the second and third segments have 1 seta and 6 setae, respectively.

Remarks

The present specimens are in full agreement with the description by Giesbrecht (1892) except for the urosome, which seems to be somewhat shorter than that figured by him. This difference may be due to the telescoping of the segments. The female is not known.

Haloptilus spiniceps (Giesbrecht, 1892)

Occurrence

Sta. 3. 6 adult females, 4.41 to 4.80 mm.
Sta. 5. 5 adult females, 4.12 to 4.99 mm.
Sta. 7. 2 adult females, 4.50 to 4.60 mm.

Remarks

This species can readily be distinguished from the other species of the genus by the short, hooked, spiniform projection of the forehead, viewed from the side.

Augaptilus spinifrons Sars, 1907
(Plate 12, figs. 1–5)

Occurrence

Sta. 5. 1 adult female, 3.55 mm.

Remarks

The female of this species can be identified by five characters: The anterior end of the body is produced into an acute spiniform process that is pointed downward (figs. 1 and 2)—

the tip of the process appears to be divided into two minute points. The rostrum consists of two slender filaments. The mandibular palp (fig. 3) is uniramous and has 4 segments; the distal segment has 2 long plumose setae. The mandibular blade is armed with 5 rostral teeth (fig. 4). The fifth leg (fig. 5) has a long seta on the posterior surface of the basis that extends beyond the end of the exopod. This seta is much longer than that figured by Sars (1925).

This species has been recorded from the Azores and off Gibraltar by Sars (1907, 1925) and from the Great Barrier Reef by Farran (1936).

FAMILY ARIETELLIDAE

Arietellus aculeatus (T. Scott, 1894)
(Plate 12, figs. 6–16)

Rhincalanus aculeatus T. Scott, 1894, p. 31, plate 2, figs. 11–24.

Arietellus setosus Giesbrecht and Schmeil, 1898, p. 124.

Arietellus aculeatus, A. Scott, 1909, p. 143, plate 44, figs. 4–7; Farran, 1929, p. 270; Wilson, 1950, p. 165.

Occurrence

Sta. 3. 1 adult male, 3.60 mm.;
1 fifth copepodid male, 2.90 mm.

This species was originally erected on the basis of a single immature male from the Gulf of Guinea and placed in the genus *Rhincalanus* (T. Scott, 1894). Afterward it was made a synonym of *Arietellus setosus* by Giesbrecht and Schmeil (1898). A. Scott (1909) found a single mature female in the *Siboga* plankton. Upon this female and the immature male, A. Scott reestablished his father's species. Farran (1929) reported a mature male from off New Zealand but gave no detailed description. The following description is from an adult male referable to this species in the present collections.

Description of Male

The total length is 3.60 mm. The proportions of the prosome to the urosome are 4:1. The first metasomal segment is separated from the cephalosome, but the fourth and fifth metasomal segments are completely fused. The forehead has a very strong spiniform process, which is curved slightly downward in lateral aspect (fig. 7). The rostrum is composed of two slender filaments, which are almost hidden between the basal portions of the antennules. The spiniform projections of the last metasomal segments are slightly asymmetrical and rather divergent, but the tips are curved slightly inward. Of these projections the right one is slightly longer, reaching to the middle of the fourth urosomal segment (fig. 6). The urosome is 5-segmented; the second to fourth segments are of nearly equal length.

The left antennule is modified for grasping the female and is 19-segmented. Figure 8 shows the arrangement of the setae and aesthetes.

The antenna (fig. 9) is composed of a rather small basipod, a 2-segmented endopod, and a 6-segmented exopod. The endopod is longer than the exopod; both are slender.

The mandibular palp (fig. 10) lacks an endopod; the basis is longer than the exopod. The mandibular blade (fig. 11) is armed with 4 large teeth, 3 of which are grouped.

The maxillule (fig. 12) has 2 inner lobes, of which the first has 5 spines and the second a single spine. The single outer lobe has 8 setae. The exopod is relatively large, with 3 setae at the apex. The endopod is absent.

The maxilla and maxilliped are similar to those of *A. setosus* as figured by Giesbrecht (1892).

The coxa in the first pair of legs (fig. 13) has an internal seta, and the basis has an internal and an external seta. The endopod is 3-segmented; the first segment has 1 internal seta, the second segment 2 internal setae, and the third segment 2 internal setae, 1 external seta, and 2 terminal setae. The exopod is also 3-segmented; the first and second segments each have 1 external spine and 1 internal seta. The third segment has 4 internal setae, 2 external spines, and a terminal spine.

The basipod of the second leg (fig. 14) has a single seta on the internal margin of the coxa. The endopod is 3-segmented; it has 1 internal seta on the first segment, 2 internal setae on the second segment, and 8 setae on the third segment. The exopod is also 3-segmented; the first and second segments each have 1 internal seta and 1 slender, curved external spine. The

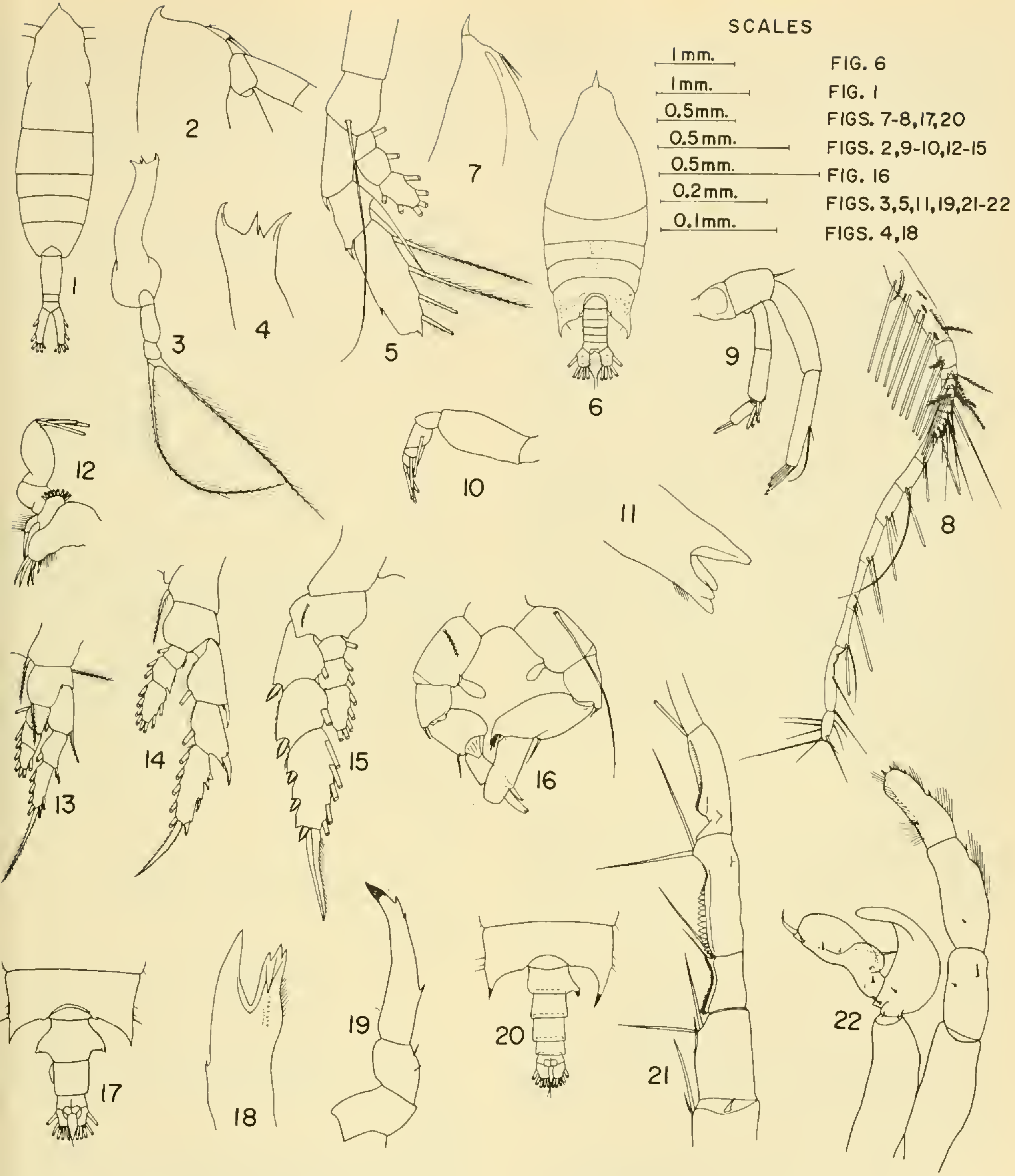
SCALES
1 mm. FIG. 6
1 mm. FIG. 1
0.5 mm. FIGS. 7-8, 17, 20
0.5 mm. FIGS. 2, 9-10, 12-15
0.5 mm. FIG. 16
0.2 mm. FIGS. 3, 5, 11, 19, 21-22
0.1 mm. FIGS. 4, 18
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PLATE 12. Figs. 1–5, *Augaptilus spinifrons*. Female: fig. 1, habitus, dorsal view; fig. 2, forehead, lateral view; fig. 3, mandible; fig. 4, mandibular blade; fig. 5, fifth leg. Figs. 6–16, *Arietellus aculeatus*. Male: fig. 6, habitus, dorsal view; fig. 7, forehead, lateral view; fig. 8, left antennule; fig. 9, antenna; fig. 10, mandibular palp; fig. 11, mandibular blade; fig. 12, maxillule; fig. 13, first leg; fig. 14, second leg; fig. 15, fourth leg; fig. 16, fifth pair of legs, posterior aspect. Figs. 17–22, *Candacia bipinnata*. Female: fig. 17, posterior part of metasome and urosome, dorsal view; fig. 18, mandibular blade; fig. 19, fifth leg. Male: fig. 20, posterior part of metasome and urosome, dorsal view; fig. 21, geniculated region of right antennule; fig. 22, fifth pair of legs, posterior aspect.

third segment has 5 internal setae, 3 small external spines, and 1 strong terminal spine almost as long as the segment.

The third and fourth legs (fig. 15) are similar. The basipod has a single seta on the posterior surface of the basis. The exopod is 3-segmented; the first and second segments each have 1 internal seta and 1 external spine; the third segment has 5 internal setae, 3 external spines, and 1 strong terminal spine nearly as long as the segment. The endopod is also 3-segmented; the first segment has 1 internal seta, and the second segment 2 internal setae. The number of setae on the third segment is 8 in the third leg and 7 in the fourth leg.

The fifth pair of legs (fig. 16) is asymmetrical. Both the right and the left legs have a 3-segmented exopod and a small, lamelliform endopod. The endopods of both legs have nearly the same shape, but the left one is slightly larger. The third exopodal segment of the left leg has a low, triangular projection on the external margin and 2 apical clawlike spines, the outer of which is larger and terminates with 2 points. The third exopodal segment of the right leg is lamelliform and lacks spines or setae.

Remarks

Because of one long frontal spiniform process, *A. aculeatus* appears to be closely related to *A. armatus* Wolfenden, 1911, which Farran (1929) considered as a probable synonym of the former. Wilson (1950), however, redescribed both sexes of *A. armatus* as a valid species.

The present specimen seems to differ only slightly from *A. armatus* described by either Wolfenden (1911) or Wilson (1950) in that the frontal process is comparatively short and both endopods of the fifth pair of legs are simple instead of forked.

Arietellus setosus Giesbrecht, 1892

Occurrence

Sta. 5. 1 adult male, 3.93 mm.
Sta. 7. 2 adult males, 4.03 to 4.12 mm.

Remarks

This species can readily be distinguished from the other species of the genus by the short and slightly curved spiniform process of the forehead and the strong spiniform projections of the last metasomal segment. These characters have been figured by Grice (1962).

FAMILY CANDACIIDAE

Candacia ethiopica Dana, 1849

Occurrence

Sta. 3. 2 adult females, 2.47 to 2.60 mm.;
2 adult males, 2.48 to 2.50 mm.
Sta. 5. 3 adult females, 2.83 to 2.97 mm.;
5 adult males, 2.47 to 2.93 mm.
Sta. 7. 5 adult females, 2.77 to 3.03 mm.;
7 adult males, 2.50 to 2.67 mm.
Sta. 9. 1 adult female, 3.00 mm.

Remarks

The female is easily distinguished from the other species of the genus by the small lateral and ventral spiniform processes of the genital segment and by the terminal segment of the fifth leg, which has 7 spines.

The male is recognized by the spiniform projection of the left posterolateral corner of the metasome; the tip of this projection is divided into 2 points. The genital segment has 2 triangular processes on the right margin. These characters have been figured by Grice (1962).

Candacia bipinnata Giesbrecht, 1889
(Plate 12, figs. 17–22)

Occurrence

Sta. 13. 3 adult females, 2.90 to 3.00 mm.;
3 adult males, 2.77 to 2.83 mm.
Sta. 15. 3 adult females, 2.84 to 2.90 mm.;
2 adult males, 2.86 to 2.94 mm.
Sta. 16. 3 adult females, 3.06 to 3.16 mm.;
5 adult males, 2.75 to 3.02 mm.

Remarks

The genital segment of the female (fig. 17) has lateral conical projections; the tips of the projections are produced into small spines. The second urosomal segment has a flaplike protrusion on the ventral margin. The male is distinguished from the other species of the genus by the shape of the last metasomal segment and the genital segment (fig. 20).

Candacia varicans Giesbrecht, 1892

Occurrence

Sta. 3. 1 adult female, 2.50 mm.
Sta. 7. 1 adult female, 2.80 mm.

Remarks

The female is recognized by the symmetrical genital segment, the fifth pair of legs, and the shape of the manibular blade (see Grice, 1962, plate 31, figs. 8, 10, and 13).

Candacia longimana Claus, 1863

Occurrence

Sta. 3. 1 adult male, 3.19 mm.
Sta. 5. 1 adult male, 3.20 mm.
Sta. 7. 1 adult male, 3.55 mm.

Remarks

The male of this species can be identified by the spiniform process on the right posterolateral margin of the metasome, the conical process on the right margin of the genital segment, and the structure of the fifth pair of legs (see Grice, 1962, plate 28, figs. 6, 8, 11, and 12).

Paracandacia bispinosa (Claus, 1863)

Occurrence

Sta. 3. 14 adult females, 1.74 to 1.91 mm.; 12 adult males, 1.88 to 1.94 mm.
Sta. 5. 20 adult females, 1.74 to 2.01 mm.; 17 adult males, 1.94 to 2.11 mm.
Sta. 7. 9 adult females, 1.84 to 1.91 mm.; 5 adult males, 2.04 to 2.11 mm.

Remarks

This species is one of the most common from the southern stations. The genital segment of the female is nearly triangular when viewed from above. Each side of the segment is produced into a small spine; the spine of the left side is longer and directed backward. The male can be distinguished by the shape of the geniculated portion of the right antennule. These characters have been figured by Grice (1962).

The species was transferred by Grice (1963) from the genus *Candacia* to his new genus *Paracandacia*.

FAMILY PONTELLIDAE

Pontellopsis regalis (Dana, 1849)
(Plate 13, figs. 1–14)

Occurrence

Sta. 3. 1 adult female, 3.20 mm.

Description of Female

The total length is 3.20 mm. The ratio of the prosome to the urosome is 4.6:1. The first metasomal segment is separated from the cephalosome. The forehead in dorsal aspect (fig. 1) is broadly rounded and has a projection over the base of the rostrum. The last metasomal segment, consisting of the fused fourth and fifth metasomal segments, is produced posterolaterally into acute spiniform processes directed backward. In dorsal aspect these processes appear to reach two-thirds the length of the genital segment (fig. 2).

The urosome is 2-segmented. The genital segment in dorsal aspect is slightly asymmetrical. Its width increases toward the posterior margin, where each side is projected posteriorly into a conical process; the right process is shorter than the left and has a minute, spiniform bristle at the apex. The anal segment and the caudal rami are symmetrical; their combined length is slightly shorter than the genital segment.

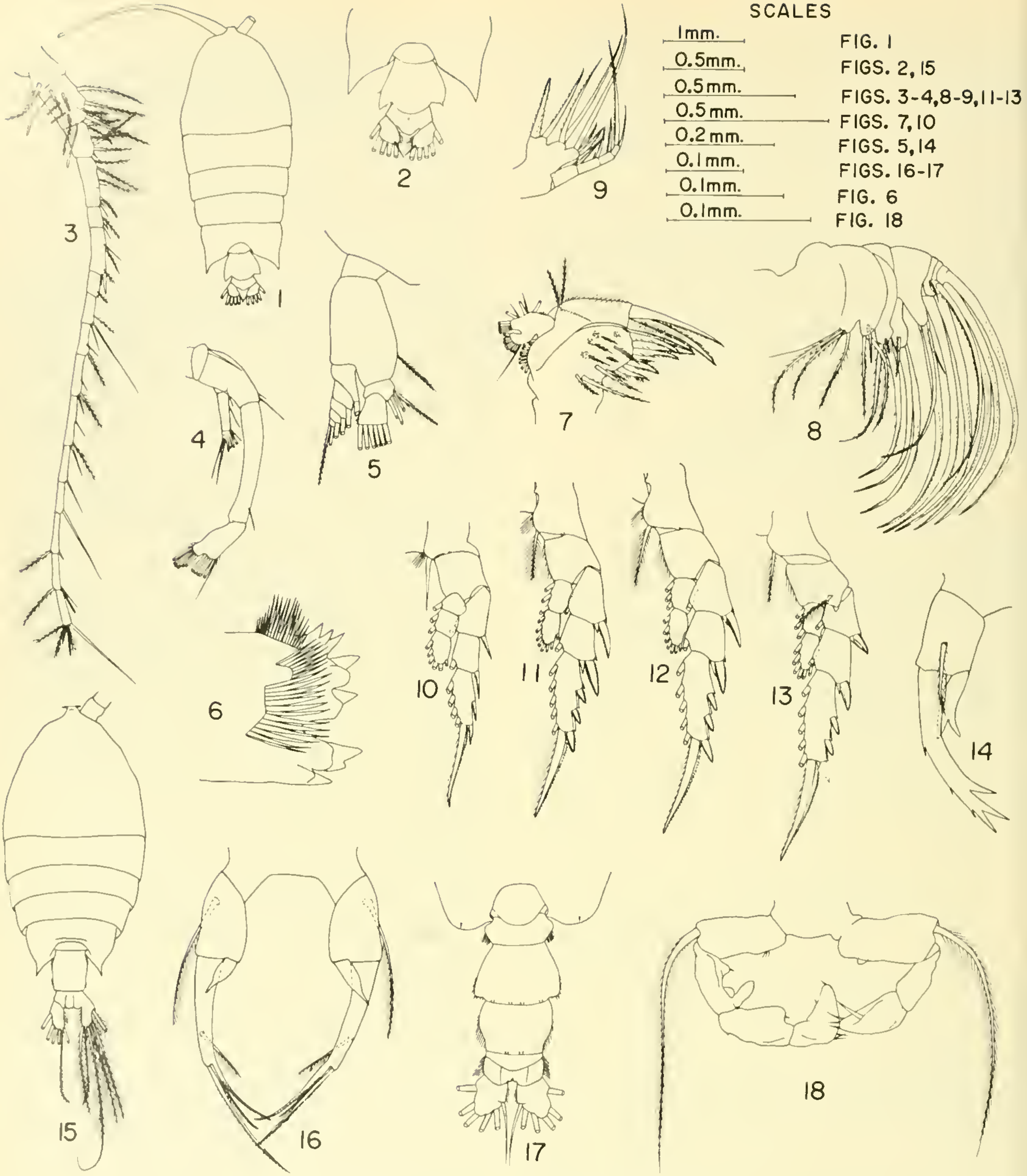
The antennule (fig. 3) is 16-segmented and reaches the middle of the second metasomal segment. The exopod of the antenna (fig. 4) is very small—about one-third the length of the endopod.

The mandibular blade (fig. 6) has five groups of teeth, in addition to three rows of strong spines on each side.

The first and second inner lobes of the maxillule (fig. 7) are well developed; the first has 6 spines along the internal margin and 10 on the posterior surface, and the second has 3 strong spines on the tip. The third inner lobe is small; it has 3 setae. The basis, endopod, and exopod are fused.

The maxilla (fig. 8) is strongly developed and has 5 lobes on the basipod. The endopod has 6 strong spines plus 1 small spine.

The maxilliped (fig. 9) consists of 1-segmented basipod and a 4-segmented endopod.


SCALES
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0.5mm. FIGS. 7,10
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PLATE 13. Figs. 1–14, *Pontellopsis regalis.* Female: fig. 1, habitus, dorsal view; fig. 2, posterior part of metasome and urosome, dorsal view; fig. 3, antennule; fig. 4, antenna; fig. 5, mandibular palp; fig. 6, mandibular blade; fig. 7, maxillule; fig. 8, maxilla; fig. 9, maxilliped; fig. 10, first leg; fig. 11, second leg; fig. 12, third leg; fig. 13, fourth leg; fig. 14, fifth leg. Figs. 15–16, *Pontellina plumata.* Female: fig. 15, habitus, dorsal view; fig. 16, fifth pair of legs. Figs. 17–18, *Acartia negligens.* Male: fig. 17, posterior part of metasome and urosome, dorsal view; fig. 18, fifth pair of legs.

The basipod is broad and has 3 lobes, which have 2, 2, 3 spines, respectively.

The basipod of the first leg (fig. 10) has a single seta on the internal margin of the coxa. The exopod is 3-segmented. Each of the first and second segments has an internal seta and an external spine. The third segment has 2 external spines, 4 internal setae, and a terminal spine that is serrated along the outer margin. The endopod is also 3-segmented. The first segment has a single internal seta, the second segment 2 internal setae, and the third segment 6 setae.

The second and third pairs of legs (figs. 11 and 12) are similar. The basipod carries a single internal seta on the coxa. The exopod is 3-segmented. Each of the first and second segments has an internal seta and a strong external spine. The third segment has 3 external spines, 5 internal setae, and a strong terminal spine that is serrated along the external margin. The endopod is 2-segmented. The first segment has 3 internal setae and 1 external seta. The second segment has 8 setae.

The fourth pair of legs (fig. 13) is similar to the third, but the basis has a seta on the posterior surface and the second endopodal segment has 7 setae instead of 8.

The basipod of the fifth leg (fig. 14) has a plumose seta on the posterior surface of the basis. The exopod and endopod each consist of a single segment. The exopod has a forked tip, a strong spine along the internal margin, and 3 small spines along the external margin. The endopod also has a forked tip; it is about one-third the length of the exopod.

Remarks

In the shape of the urosome the present specimen is not in full agreement with the description given by Giesbrecht (1892). According to A. Fleminger (personal communication), however, it is not outside the usual variability shown by the species.

Pontellina plumata (Dana, 1849)
(Plate 13, figs. 15–16)

Occurrence

Sta. 7. 1 adult female, 1.94 mm.

Remarks

A single female referable to the above species was in the present collections. The specimen agrees in every detail with the description and figures given by Giesbrecht (1892) except for the structure of the endopod of the fifth leg (fig. 16). The sizes of the right and left endopods are slightly unequal, and each is single-pointed, not forked.

FAMILY ACARTIIDAE

Acartia danae Giesbrecht, 1889

Occurrence

Sta. 3. 1 adult female, 1.20 mm.

Remarks

The female can be recognized by the large spine on the first segment of the antennule, the pointed posterolateral corners of the metasome, and the structure of the fifth pair of legs.

Acartia negligens Dana, 1849
(Plate 13, figs. 17–18)

Occurrence

Sta. 3. 3 adult females, 1.23 to 1.30 mm.
Sta. 5. 5 adult females, 1.22 to 1.28 mm.; 1 adult male, 1.15 mm.
Sta. 7. 7 adult females, 1.25 to 1.28 mm.; 1 adult male, 1.18 mm.

Remarks

In the female, the fifth pair of legs is somewhat similar to that of *A. danae*, but the posterolateral corners of the metasome are rounded and have small spines. The shape of the urosome and the fifth pair of legs of the male can best be described by reference to figures 17 and 18.

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A RAPID METHOD OF TAGGING FISH[1]

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A unique tagging procedure has been devised that requires but two persons, is rapid, and provides accurate permanent records that can be rechecked as many times as necessary. Methods used up to this time require several men, and the records obtained are only temporary and often inaccurate.

The Division of Fish and Game, Department of Land and Natural Resources, State of Hawaii, is now tagging akule (bigeye scad), *Trachurops crumenophthalmus*, for studies of growth and migration.

Generally, our tagging method is an extension and modification of fish measuring techniques described by Wollaston (1928), Thompson (1929), and recently by Joeris (1959), who used a measuring board to which plastic strips (exposed or outdated X-ray film strips) were attached. The fish is laid on the measuring board with its snout against a stopblock, and the length is recorded by punching a hole in the film. The method described here involves the same general technique except that X-ray films are also specially prepared to hold and dispense tags in numerical order and to retain paired information on tag numbers and length of fish tagged.

The adaptation of X-ray film to fulfill the method's requirements was accomplished by painting stripes on the film and placing a tag with each stripe. It involves the association of tag, tag number, and length of fish represented by a perforation on the film in the striped area. To adapt the film, each exposed X-ray film plate (obtained from local hospitals without cost) is prepared with several equally spaced horizontal 12.5-mm. wide yellow stripes spray-painted through a template on the film. At the end of each stripe the film is slit to hold the modified plastic internal anchor tag used on *T. crumenophthalmus* (Sakuda, 1966); the tags are in numerical order from the top to the bottom of the film. The tag numbers are written on the first and last stripes with a china-marking pencil (fig. 1). The size of the X-ray film, number of stripes, and spacing between stripes, depend on the size of fish to be tagged. For akule, a plate 36.0 by 43.2 cm. is used; it carries 15 stripes. Other types of tags (e.g. dart, spaghetti, or Petersen disk) may be attached to the tagging plate with masking tape.

The tagging plates require a flat surface for their use; a table with a 12.5-mm.-thick cork top and a stopblock along one edge served this purpose. The tagging plate is butted firmly against the stopblock and securely pinned to the table, and the immobilized fish is laid along the horizontal stripe with its snout against the stopblock. Length is then recorded by perforating the stripe with a dissecting needle. The corresponding tag at the end of the stripe is then removed from the plate and inserted into the body cavity through a small incision on the side of the fish.

To minimize handling of the fish, a holder is also used in the tagging. It is constructed of 1.5-mm.-thick clear plastic sheet, 30.5 cm. long and 6.3 cm. wide, with a 12.5-mm.-wide lengthwise slot to match the horizontal stripe on the tagging plate. When placed over the tagging plate, the holder is manipulated to center the fish over the stripe and in position for the length measurement to be punched. A 6.2-mm.-thick sheet of polyurethane foam, 23.0 cm. long and 6.3 cm. wide, is glued to the upper surface of the holder to provide a soft, moist bed for the fish during tagging. A piece of nylon window screen the size of the holder is glued to the undersurface of the holder to reduce adhesion of the holder to the tagging plate. Fish length is recorded by punching a hole into the tagging plate through the foam sheet and screen.

The tagging plates are stored in numerical order in cardboard boxes painted with epoxy resin. Upon completion of a day's tagging, the

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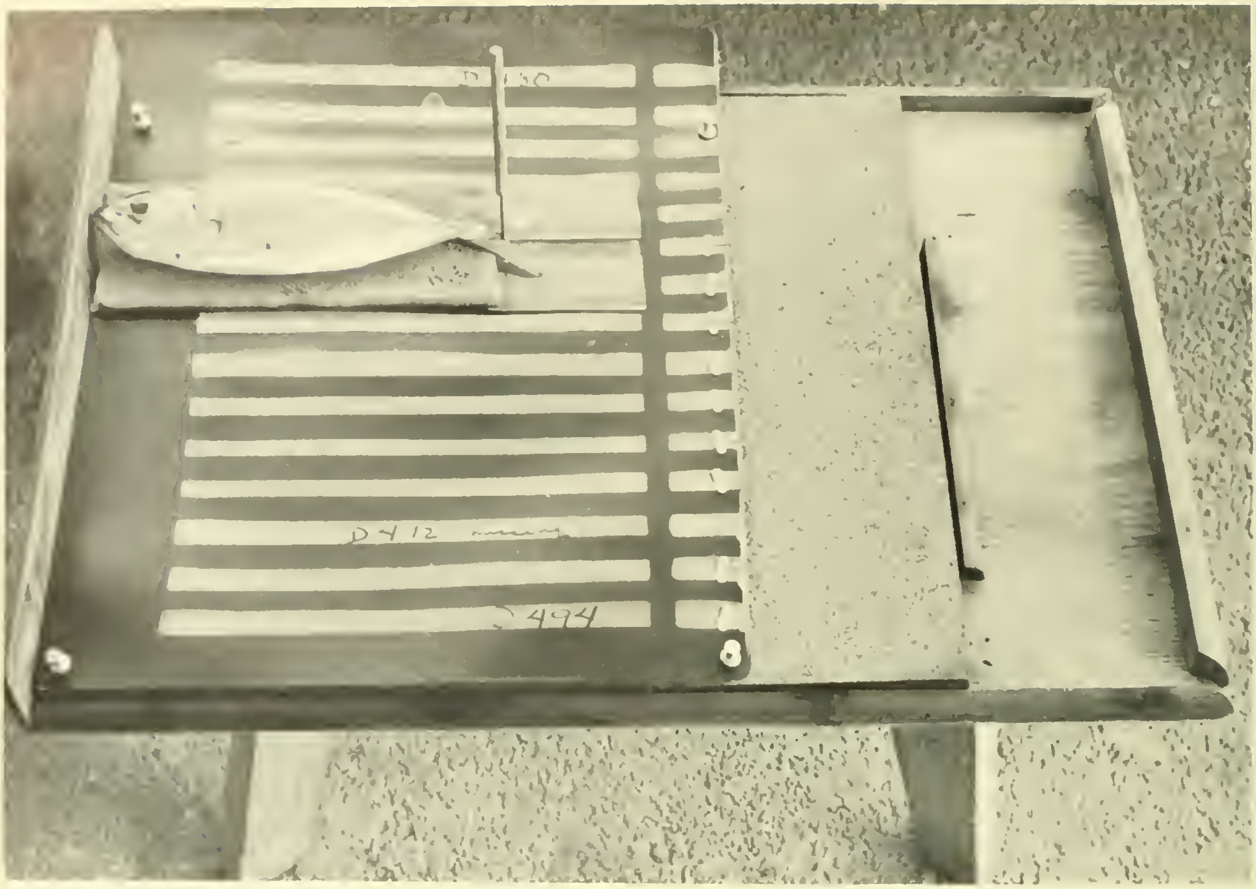

FIGURE 1.—The fish tagging equipment in use.

plates are washed and dried, and tag numbers and length measurements are recorded. Fish lengths are read off the tagging plates with a T–square ruler.

With experience in judging the time required to immobilize akule, two men (a tagger and an anesthetist) have tagged about 100 fish per hour. The rapidity and relative ease of tagging by this method also afford time for additional care in handling the fish. Use of the X-ray-film tagging plate has three other advantages over the usual tagging procedure: it (1) eliminates reading and recording the tag numbers and fish-length measurements during the tagging; (2) minimizes errors (misreading, misrecording, and digit bias) during the tagging; and (3) provides permanent length records that can be rechecked later.

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MIGRATION AND DISTRIBUTION OF PINK SALMON SPAWNERS IN SASHIN CREEK IN 1965, AND SURVIVAL OF THEIR PROGENY

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ABSTRACT

The escapement of 14,813 pink salmon (*Oncorhynchus gorbuscha*) to Sashin Creek, southeastern Alaska, in 1965, followed by the emergence of 2.2 million fry, or 18 percent of the potential egg deposition, represented a relatively high survival of eggs and alevins in a stream, where the long-term average is 7 percent. This high survival was predicted from an established relation between survival of eggs and alevins and the time the parents entered Sashin Creek to spawn.

The spawning ground was divided into three areas—upper, middle, and lower—to study density of spawners and survival of their progeny. Density in 1965 was higher in the middle and upper areas than in the lower. From egg deposition to fry emergence, survival was estimated to be 23 percent in the upper area, 18 percent in the middle area, and 14 percent in the lower area.

The instantaneous rate of mortality remained relatively unchanged from deposition of eggs to emergence of fry in the upper and middle areas. In the lower area, mortality was relatively high during spawning and low between spawning and hatching of eggs. Much of the mortality throughout the stream was traced to the disappearance of eggs and alevins. Factors causing this disappearance included retention of eggs, superimposition of redds, predation, and turbulent water. A drought during spawning retarded development of embryos and caused considerable mortality.

The numbers of pink salmon (*Oncorhynchus gorbuscha*) fluctuate drastically from year to year, and knowledge of the natural processes that cause the fluctuations is required if the resource is to be managed effectively. To evaluate mortality of pink salmon in fresh water, the Bureau of Commercial Fisheries has studies in Sashin Creek, a small spawning stream on Baranof Island, southeastern Alaska.

Adult pink salmon entering Sashin Creek have been counted each year since 1934, and fry leaving have been counted since 1941. Adults have numbered from 8 to 92,085 and fry from 50 to 5,940,300; fresh-water survival has ranged from 0.06 to 21.75 percent of potential egg deposition (table 1).

Only a small portion of Sashin Creek can be used by salmon spawners. Although the Creek is about 4,000 m. long, a waterfall 1,200 m. from the head of tidewater prevents further upstream movement of fish. Spawning is limited in a narrow canyon that extends 300 m. downstream from the waterfall and in the intertidal zone, where the gradient is steep and the bottom is mostly bedrock. The main spawning ground (13,629 m.^{2}) lies between the intertidal zone and the canyon.

Four factors that affect survival of pink salmon in Sashin Creek have been discussed by Merrell (1962) and McNeil (1966): (1) time of migration of spawners, (2) distribution of spawners, (3) density of spawners, and (4) weather. To clarify further the relation of these and possibly other factors to survival of eggs, alevins, and fry in Sashin Creek, I studied a relatively large run of pink salmon that spawned there in late August and in September 1965. Survival from deposition of eggs to emergence of fry was estimated in three areas that included 97 percent of the total spawning ground used by spawners in years of large escapements.

In this paper, I describe the migration, distribution, and density of pink salmon spawners in the summer of 1965, and the survival of their progeny in fresh water. Also, I discuss: (1) the relation of survival of eggs and alevins to time of spawning of adults, (2) variation among stream areas in density of fry, (3) relation of water quality (primarily concentration of dissolved oxygen) to survival and development of embryos, (4) disappearance of eggs and alevins from spawning beds, and (5) seasonal variation in mortality in spawning beds.

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Table 1.—*Number of adult pink salmon in each escapement, potential egg deposition, number of fry produced, and fresh-water survival for brood years 1934–65, Sashin Creek, southeastern Alaska*

Brood year [1]	Adults in escapement	Potential egg deposition [2]	Fry produced	Fresh-water survival
	Number	*Number*	*Number*	*Percent*
1934	7,917			
1935	6,323			
1936	5,364			
1937	9,085			
1938	6,467			
1939	16,830			
1940	53,594	52,858,000	3,399,900	6.43
1941	84,303	88,678,000	1,024,300	1.16
1942	92,085	78,894,000	674,000	0.85
1943	14,883	14,980,000	227,800	1.52
1944	4,050	3,904,000	105,606	2.71
1945	5,465	5,062,000	43,100	.85
1946	933	736,000	1,200	.16
1947	1,486	1,330,000	27,600	2.07
1948	597	516,000	9,100	1.76
1949	4,902	4,800,000	176,200	3.67
1950	112	86,000	50	.06
1951	4,366	4,062,000	412,500	10.15
1952	45	(3)	740	----
1953	1,164	1,284,000	95,400	7.43
1954	21	12,000	660	5.48
1955	9,267	10,286,000	266,200	12.31
1956	933	1,018,000	5,040	.50
1957	2,834	2,588,000	562,900	21.75
1958	217	174,000	10,700	6.13
1959	35,391	40,379,000	5,332,400	13.21
1960	162	(3)	480	
1961	28,759	29,425,000	5,940,300	20.19
1962	8	8,000	100	1.20
1963	16,757	16,640,000	3,256,300	19.57
1964	[4] 2,193	2,230,000	[5] 310,000	13.91
1965	14,833	12,668,000	[5] 2,235,000	17.92

[1] The term "brood year" refers to the year of spawning.

[2] Based on 2,000 eggs per female except when actual fecundity was calculated in 1942 (1,936 eggs), 1957 (1,988 eggs), 1959 (2,040 eggs), 1960 (1,903 eggs), 1961 (1,991 eggs), 1963 (1,908 eggs), 1964 (1,709 eggs), and 1965 (1,782 eggs).

[3] An attempt was made to destroy the spawners.

[4] Natural escapement (327) was reinforced by introduction of 1,866 adults.

[5] Fry weir was not functioning; estimate based on number of preemerged alevins in spawning beds.

MIGRATION, DISTRIBUTION, AND DENSITY OF SPAWNERS

Fresh-water survival of pink salmon eggs and alevins in Sashin Creek is inversely related to the time of migration of the spawners (Skud, 1958; Merrell, 1962). Because pink salmon are mature when they enter Sashin Creek, early entry into the stream means early spawning and late entry gives late spawning. The date by which 50 percent of all of the spawners had entered the Creek is used in this paper to index the time of spawning. In 1965, 50 percent of the spawners had entered the Creek by August 26, which was the fourth earliest date of record. I had expected, therefore, that survival of the eggs and alevins would be high.

The distribution and density of spawners in 1965 were analyzed to determine if spawners concentrated in areas that afforded the best habitat for embryos and alevins. Ninety-seven percent (13,084 m.^{2}) of the Sashin Creek spawning ground was divided into three areas—upper (2,945 m.^{2}), middle (4,067 m.^{2}), and lower (6,072 m.^{2}). The upper area has a relatively high gradient and coarse materials in the bed; the middle area has an intermediate gradient and medium-sized materials; and the lower area has a low gradient and relatively fine materials (table 2).

Table 2.—*Average gradient and size composition of bottom materials*[1] *in three areas in Sashin Creek*

Area	Average gradient	Bottom composed of—		
		Coarse particles [2]	Medium particles [2]	Fine particles [2]
	Percent	*Percent*	*Percent*	*Percent*
Upper	0.7	81	16	3
Middle	.3	61	26	13
Lower	.1	47	36	17

[1] Procedures for sampling bed materials to measure size composition were described by McNeil and Ahnell (1964).

[2] Coarse particles are >12.7 mm. diameter; medium particles are 1.68 to 12.7 mm.; fine particles are <1.68 mm. diameter.

In years before 1965, when spawners were abundant they used the entire Sashin Creek spawning ground but concentrated in the middle area. Nevertheless, the upper area produced more fry per unit area of streambed than the middle or lower area (Merrell, 1962; McNeil, 1966). When spawners were scarce, they usually concentrated in the lower area and did not use the upper area at all. The failure of spawners to use the potentially most productive upper area raises important questions about factors that control their distribution.

In 1965, 14,813 pink salmon spawners, including 7,109 females, entered Sashin Creek. Two hundred of the females were captured as they passed the weir and were tagged with plastic Petersen disks 1.6 cm. in diameter, fastened below the dorsal fin. Fifty fish were tagged with white disks on August 18, 50 with red disks on August 24, 50 with yellow disks on August 28, and 50 with green disks on September 12. The dates of release of the tagged females were selected to ensure representation of the early, middle, and late portions of the migration to fresh water. Seven percent of the total number of females (7,109) had entered Sashin Creek before the first date of tagging (August 18); 37 percent before the second date (August 24); 70 percent before the third date (August 28); and 95 percent before the fourth date (September 12). An observer on foot counted tagged and untagged females in each area and recorded their location. Only females were counted because they determine potential egg deposition.

The females were easy to count on the spawning ground because they remained near the site of their redds from the beginning of spawning until they died. I evaluated this behavior, which is typical of spawning females, by observing 14 tagged females that were spawning in a 100-m.-long section of Sashin Creek. The locations of the 14 females were determined twice daily with a transit and stadia and were plotted on a detailed map. The average longevity on the spawning ground of the 14 females was 11.5 days (range 3 to 20 days). The average size of the area occupied was 3.8 m.^{2} (1.4 m. wide by 2.7 m. long). The smallest area occupied, 0.6 m.^{2}, was for a fish that lived only 3 days after establishing a site, and the largest, 17.3 m.^{2}, was for a fish that lived 9 days. All died near their redds.

One method of estimating the number of females that spawned in an area was to sum the daily counts of untagged females and divide by their average longevity. The daily counts were summed by fitting a curve to the number of untagged females counted each day and measuring the area under the curve (examples are given by McNeil, 1964a and 1964b). Average longevity was estimated from daily observations of tagged females. One day was added to the number of days individual tagged females were observed because I assumed they occupied the spawning ground one-half day before they were first observed and one-half day after they were last observed.

Estimates of the number of females in each area based on summed daily counts and average longevity were 2,040 in the upper area, 3,095 in the middle, and 3,051 in the lower. I assumed that 97 percent of the total number of females spawned in the three areas, and my estimate for the whole stream was 8,439 females, or 118.7 percent of the number counted at the weir. The estimates for each area were, therefore, adjusted by dividing by 1.187. The resulting estimates were 1,719 females in the upper area, 2,607 in the middle, and 2,570 in the lower.

A second method of estimating the number of females in each area was based on the occurrence of tagged females. I assumed that tagged and untagged females were distributed similarly. Of the 200 tagged females released, 184 (92 percent)[1] were recorded in the study areas: 45 in the upper area, 64 in the middle, and 75 in the lower. On the further assumption that 97 percent of the females counted at the weir spawned in the three areas and were distributed in the same proportion as the 184 tagged females, I estimated that 1,689 females spawned in the upper area, 2,399 in the middle, and 2,813 in the lower.

The density of females spawning in each area was calculated by dividing the total number of females by the area of spawning bed. The estimates of density of females in each area by each of the two methods for estimating the number of females agreed closely (table 3) and indicated that density of spawners was about the same in all areas. Although the observed number of tagged females in each area was not significantly different from the expected number calculated from an assumed uniform density of tagged females (table 4), the conclusion that the average density of females was identical among the areas is less attractive than the conclusion that small differences existed. I will use, therefore, the mean of the two estimates of density for each area (table 3) as the best (most probable) estimate of density in my calculations of potential egg deposition.

TABLE 3.—*Density of female pink salmon spawning in three areas of Sashin Creek, based on observations of untagged females (summed daily counts) and tagged females*

Area	Females per square meter, based on—		Mean of the two estimates
	Observations of untagged females	Observations of tagged females	
	Number	*Number*	*Number*
Upper	0.58	0.57	0.58
Middle	.64	.59	.62
Lower	.42	.46	.44

TABLE 4.—*Numbers of tagged female pink salmon observed in three areas in Sashin Creek and the expected number, based on an assumed equal density*

Area	Female pink salmon	
	Observed	Expected
	Number	*Number*
Upper	45	41.4
Middle	64	57.2
Lower	75	85.4

χ^2 (2 d.f.) = 2.39 (P, 0.30).

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[1] Additional tagged females may have spawned in the study areas but were not seen.

SURVIVAL OF EGGS AND ALEVINS

Estimates of survival of eggs and alevins in this paper pertain to three periods in the fresh-water life of 1965 brood year pink salmon:

Period	*Months*
1. Egg deposition (late August through September)	1. 3
2. Egg deposition and hatching (October through mid-November)	1. 7
3. Hatching and fry emergence (late November into late March)	4. 2
Total	7. 2

Survival in the nth period is calculated by:

$$S_1 \cdot S_2 \quad \cdot \quad \cdot \quad \cdot \quad S_n = S \tag{1}$$

$$S_n = \frac{S}{S_1 \quad \cdot \quad S_2 \quad \cdot \quad \cdot \quad \cdot \quad S_{(n-1)}} \tag{2}$$

The symbol S is total survival from beginning of spawning to any selected date, and an estimate of S ($\hat{S}$) must account for dead eggs and alevins that may have disappeared from the population before the date of sampling. The estimate must also give a value $\hat{S} \leq 1.0$. To satisfy these requirements, the estimate of survival is calculated from:

$$\hat{S}_j = \frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} \cdot \frac{\sum_{i=1}^{k} a_{ij}}{\sum_{i=1}^{k} T_{ij}} \tag{3}$$

with the condition that

$$\frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} \leq 1.0 \tag{4}$$

In equations (3) and (4),

i designates an individual sampling ($i=1$ to k),
j designates an individual area ($j=1$ to 3),
a_{ij} is the number of live eggs and alevins collected at the ith point of the jth area,
T_{ij} is the total number of eggs and alevins (live and dead) collected at the ith point of the jth area,
e_j is the average potential egg deposition in the jth area, and
$\hat{S}_j$ is an estimate of S for the jth area.

For the case where

$$\frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} < 1.0$$

equation (3) reduces to

$$\hat{S}_j = \frac{\frac{1}{k}\sum_{i=1}^{k} a_{ij}}{e_j} \tag{5}$$

I used equation (5) in an earlier paper (McNeil, 1966) to estimate survival of pink salmon in Sashin Creek.

The average density of eggs and alevins was estimated in each area from samples obtained with hydraulic sampling equipment described by McNeil (1964a). The points sampled, each representing 0.1 m.^{2} of the streambed, were selected randomly within the three study areas with the aid of tables of random numbers. Eggs were collected after spawning (September 29), and eggs and alevins were collected during hatching (November 20) and before emergence (March 26).

In calculating $\hat{S}_j$ (equation 3 or 5), I assumed that the number of eggs collected at each point was 93 percent of the number actually present at the time of sampling (McNeil, 1964a). Potential egg deposition was calculated by multiplying the average fecundity by the estimated average number of females that had spawned per square meter (table 3). The average fecundity, based on 20 randomly selected unspawned females taken at the weir on the four dates females were tagged, was estimated to be 1,782 eggs.

Estimates of survival from August 20 (beginning of spawning) to September 29, November 20, and March 26 are given for each area in table 5. These estimates were calculated directly from equation (3).

The estimated number of eggs per square meter in the middle area at the end of spawning was greater than the estimated potential egg deposition (table 5). Two sources of error could have contributed to this discrepancy: (1) Potential egg deposition may have been underestimated, or (2) the number of eggs at the end of spawning may have been overestimated.

The use of an area by spawning salmon can be indexed in two ways—directly by observing the density of spawners (table 3) and indirectly by

TABLE 5.—*Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and survival of 1965 brood pink salmon in three areas of Sashin Creek*

Area	Potential egg deposition per square meter: Mean	Potential egg deposition per square meter: 90-percent confidence limits of mean	Period beginning August 20 and ending—	Eggs and alevins per square meter: Combined live and dead: Mean	Eggs and alevins per square meter: Combined live and dead: 90-percent confidence limits of mean	Eggs and alevins per square meter: Ratio of live to combined live and dead: Mean	Eggs and alevins per square meter: Ratio of live to combined live and dead: 90-percent confidence limits of mean	Calculated survival
	Number	*Number*		*Number*	*Number*	*Percent*	*Percent*	*Percent*
Upper	1,034	±72	September 29	966	±216	84	±5	78
			November 20	711	±191	86	±5	59
			March 26	433	±153	54	±16	23
Middle	1,105	±77	September 29	1,504	±312	86	±4	[1] 86
			November 20	765	±222	80	±8	55
			March 26	428	±112	47	±14	18
Lower	784	±55	September 29	539	±180	60	±16	[2] 41
			November 20	549	±214	71	±13	[2] 50
			March 26	357	±95	30	±13	14

[1] This estimate is uncorrected for egg retention. The estimate corrected for egg retention is 82 percent.

[2] These estimates do not differ significantly and are averaged to give 46 percent survival for each date.

measuring the presence of eggs in sampling units at the end of spawning. To measure the presence of eggs, I classified samples with more than three eggs and alevins as points used by spawners and those with fewer eggs as unused. The classification of sample points with three or fewer eggs and alevins as unused is arbitrary, but some small value greater than zero helps correct for the presence of drifted eggs at points not actually used by spawners.

It is probable that the density of eggs in the middle area at the end of spawning was overestimated. The percentage of samples containing more than three eggs and alevins (table 6) did not change significantly for any area from immediately after spawning (September 29) to hatching (November 20). The percentages of samples with more than three eggs or alevins were similar in the upper and middle areas in both September and November, and these similar measures of use in the two areas agree with observed densities of females. Furthermore, the upper and middle areas were similar in terms of the density of eggs and alevins in both November and March (table 5). The potential egg deposition was also about equal in the two areas, and together these observations support strongly the conclusion that density of eggs was overestimated in the middle area at the end of spawning.

Relatively few eggs were unspawned in the body cavities of females. Spawned females retained 5 percent of the potential egg deposition (based on an examination of 173 females).

TABLE 6.—*Percentage of 0.1 m.² sampling units in three areas in Sashin Creek with more than three eggs and alevins, after spawning and during hatching*

Study area	Sampling units with more than three eggs or alevins—: After spawning (September 29): Mean	Sampling units with more than three eggs or alevins—: After spawning (September 29): 90-percent confidence limits of the mean	Sampling units with more than three eggs or alevins—: During hatching (November 20): Mean	Sampling units with more than three eggs or alevins—: During hatching (November 20): 90-percent confidence limits of the mean
	Percent	*Percent*	*Percent*	*Percent*
Upper	66	±8	68	±9
Middle	73	±7	68	±9
Lower	50	±8	47	±10

Estimates of survival at the end of spawning include allowance for 5 percent retention of eggs by females in the upper and lower areas. In the middle area, however, the density of live and dead eggs at the end of spawning was calculated to be 100 percent of potential egg deposition (equation 3). This estimate is too high and requires further correction for the retention of eggs by females. Because only 95 percent of potential egg deposition was voided during spawning, the estimated 86 percent of live eggs in the middle study area in late September (table 5) pertains to 95 percent (or less) of potential egg deposition. The survival estimate corrected for egg retention is, therefore,

$$0.95 \times 0.86 = 82 \text{ percent.}$$

Correction is also required for two estimates of survival in the lower area where survival was estimated to increase from 41 percent in September to

50 percent in November. Because the difference between 41 and 50 percent survival is not statistically significant, I assume that no mortality occurred in the lower area between September 29 and November 20 and use the average of the two estimates, 46 percent survival, for the spawning period through November 20.

Equation (2) was used to calculate survival in each period. Table 7 gives the results of these calculations.

Instantaneous mortality coefficients corresponding to survival percentages given in table 7 were also calculated. The equation (McNeil, 1966) is:

$$M_{jn} = \frac{-ln(S_{jn})}{t} \qquad (6)$$

where M_{jn} is the mortality coefficient for the jth area and nth period,

S_{jn} is survival for the jth area and nth period, and

t is time.

In computing values of M, the unit of time is taken as 1 month. Thus, $t=1.3$ for period 1; 1.7 for period 2; and 4.2 for period 3. The values of M for each area and period are given in table 8.

Table 7.—*Survival of pink salmon of the 1966 brood year in three areas in Sashin Creek*

Study area	Survival from—			Total survival
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)	
	Percent	*Percent*	*Percent*	*Percent*
Upper	78	76	39	23
Middle	82	67	33	18
Lower	46	100	30	14

Table 8.—*Instantaneous mortality coefficients for pink salmon of the 1965 brood year in three areas in Sashin Creek*

Area	Instantaneous mortality coefficient from—		
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)
Upper	0.19	0.16	0.23
Middle	.20	.24	.29
Lower	.60	.00	.30

Changes in the number of live eggs and alevins in each area and in the entire stream are shown in figure 1. The numbers declined in the upper and middle areas at nearly uniform rates in periods 1, 2, and 3. In the lower area, the numbers declined sharply in periods 1 and 3 but did not decline in period 2. Fry were not counted at the weir in the spring of 1966 because it had been damaged in late winter, but I have assigned 100-percent survival to period 4 (dotted extensions of the curves in figure 1) in all areas on the basis of previous years' data from Sashin Creek (table 9).

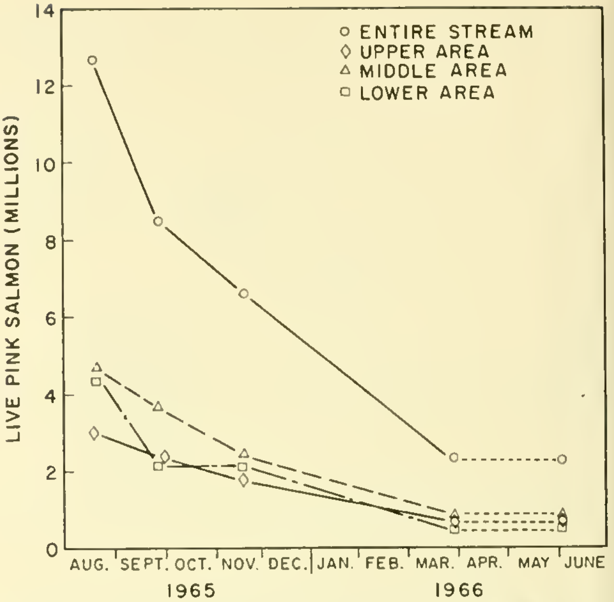

Figure 1.—Number of live pink salmon of the 1965 brood year in three areas of Sashin Creek and in the entire stream at beginning and end of four periods in fresh water. The dotted extensions in April and May are for the period of fry migration and are discussed in the text.

Although the density of fry varied among the three areas, the number of fry produced in each was about the same because of differences in sizes

Table 9.—*Comparison of estimates of survival of pink salmon fry in Sashin Creek before the fry emerge (hydraulic sampler) and at the time they migrate (weir), 1959-63*

Brood year	Estimates of survival	
	Hydraulic sampler	Weir
	Percent	*Percent*
1959	11.0	13.2
1960	(1)	
1961	21.4	20.2
1962	0.0	1.2
1963	20.7	19.6
Mean	13.3	13.6

[1] No estimate.

of the areas. The upper area had the highest number per square meter (228), the middle area the next highest (197), and the lower area the lowest (104).

RELATION OF SURVIVAL OF EGGS AND ALEVINS TO TIME OF SPAWNING OF ADULTS

The observed relation of fresh-water survival to the date by which 50 percent of the spawners entered Sashin Creek is shown in figure 2. The regression line in the figure is fitted to points for 20 brood years in the period 1940–64. Four years (1952, 1954, 1960, and 1962) were excluded from the regression because potential egg deposition was very meager (12,000 eggs or less) and one year (1964) because the adults were transplanted to the creek.

Fresh-water survival has exceeded that of the 1965 brood year in only three other brood years—1957, 1961, and 1963. In each year 50 percent of the spawners had entered the stream on or before August 26, the "index date" of stream entry for 1965. The date was August 22 in 1957 (22-percent survival); August 13 in 1961 (20-percent survival); and August 26 in 1963 (20-percent survival).

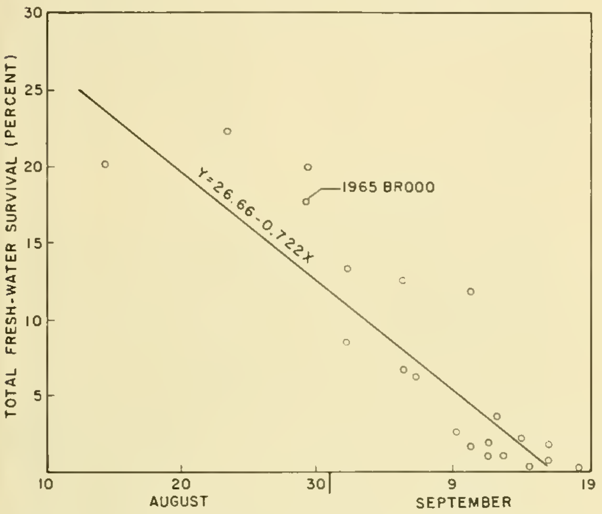

FIGURE 2.—Relation of fresh-water survival of pink salmon in Sashin Creek to date by which 50 percent of spawners entered the stream. The curve $Y=26.66-0.722X$ was fitted by least squares, $X=0$ corresponds to August 10. Relation of the 1965 brood year to the fitted regression is shown.

The predicted fresh-water survival of the 1965 brood year based on the regression line in figure 2 was 15 percent. The estimated survival based on the number of alevins collected with a hydraulic sampler (McNeil, 1964a) before the fry emerged from the streambed was 18 percent. An estimated 2,235,000 fry were produced. Although I could not compare this figure with a count of fry at the weir in the spring of 1966, survival estimated with the hydraulic sampler has agreed closely with survival estimated at the weir (table 9).

It is not entirely clear why fresh-water survival of pink salmon should be high in Sashin Creek when spawners enter early. Merrell (1962) hypothesized that embryos from eggs deposited late in the spawning season fail to develop sufficiently before the onset of cold weather and that embryos of retarded development are more sensitive to adverse effects of cold water than are more developed embryos. High mortality of pink salmon in streams tributary to the White and Barents Seas in 1960 was attributed to late spawning (Azbelev, Surkov, and Yakovenko, 1962).

Laboratory experiments indicate that exposure of salmon eggs to cold water soon after fertilization is detrimental, and this effect may partly explain why late spawning is less successful than early spawning. Eggs of sockeye salmon (*O. nerka*) held at an initial incubation temperature of 7° C. experienced higher mortality than eggs held at 10°, 13°, and 16° C. (Andrew and Geen, 1960), and early exposure of salmon eggs to temperatures of 1° and 2° C. can be lethal (Seymour, 1956; Combs and Burrows, 1957; Efimov, 1962). If incubation temperatures are high enough initially, subsequent reduction to near freezing is not always harmful, but the duration of initial exposure to warm water is important. Seymour (1956) incubated eggs of chinook salmon (*O. tshawytscha*) 2 and 3½ weeks in warm water before exposing them to cold water. He found that eggs reared 2 weeks in warm water had a high mortality when exposed to cold water, whereas eggs reared 3½ weeks in warm water had a low mortality. Additional studies would be required to determine the effect of water temperature on the survival of pink salmon eggs in Sashin Creek and whether warm water during spawning is generally necessary for high survival.

VARIATION AMONG STREAM AREAS IN DENSITY OF FRY

When pink salmon spawners are abundant in Sashin Creek, the entire spawning ground is used intensively; but the largest number of fry per square meter comes usually from the upper area. This fact was discovered first for the 1959 brood fry (Merrell, 1962), and I observed a similar difference in subsequent years when spawners were abundant. The numbers of fry per square meter in the three areas for 4 brood years were as follows (data for the 1959 brood from Merrell, 1962):

Brood year	Lower area	Middle area	Upper area
1959	135	250	325
1961	225	605	600
1963	174	268	360
1965	104	197	228
Mean	160	330	378

Even though the upper area can potentially produce more fry per unit area than the lower or middle area, observations each year since 1958 show that spawners do not concentrate there. In 1965, 14,833 fish (both sexes) spawned at about equal density in the upper and middle areas and at somewhat lower density in the lower area (table 3). In 1964, when the number of spawners was only 2,193, they were concentrated in the lower area, and relatively few were in the upper area (Smedley and McNeil, 1966). In 1963, Sashin Creek had 16,757 spawners, and the number of females per square meter was 50 percent greater in the middle area than in the upper or lower area (McNeil, 1966). Only eight pink salmon spawned in 1962; no observations were made on their distribution. In 1961, 28,759 spawners were distributed fairly uniformly throughout the spawning ground (McNeil, Wells, and Brickell, 1961). Because an attempt was made to destroy the run in 1960, no observations were made on distribution of spawners that year. Data from Merrell (1962) indicated that in 1959, when 35,391 were present, the number of females per square meter in the middle area was at least twice that in the lower or upper. Spawners were scarce in 1958 (217), and they concentrated in the lower area (Merrell, 1962).

The distribution of spawners in Sashin Creek may depend somewhat on the time of spawning. Tagged females in 1963 (table 5 of McNeil, 1966) and 1965 (table 10) "shifted" downstream after the midpoint of spawning: early spawners tended to concentrate in the upper and middle areas and late spawners in the lower area.

TABLE 10.—*Expected and observed numbers of early and late-spawning tagged female pink salmon in three study areas in Sashin Creek, 1965*

[Tagged spawners that first occupied the spawning ground by August 31 were designated as "early"; tagged spawners that occupied the spawning ground September 1 and later were designated as "late"]

Study area	Early spawners		Late spawners	
	Expected	Observed	Expected	Observed
	Number	*Number*	*Number*	*Number*
Upper	25	30	20	15
Middle	36	41	29	24
Lower	41	31	33	43
Total	......	102	....	82

x^2 (2 d.f.) = 9.27 (P, 0.01).

In an earlier paper (McNeil, 1966) I attributed the downstream shift from the upper area in 1963 to turbulent water caused by heavy rainfall in the latter half of the period of spawning (4.5 cm. per day average from September 3 to 29, 1963); but in 1965, rainfall in September averaged less than 0.2 cm. per day, and the streamflow remained low throughout the latter half of the period of spawning—a condition opposite to 1963.

It now appears that late spawners are less inclined to occupy upstream spawning beds of Sashin Creek than are the early spawners, regardless of waterflow. My earlier interpretation of the cause of the downstream shift of the late spawners now appears to be incorrect.

RELATION OF WATER QUALITY TO SURVIVAL AND DEVELOPMENT OF EGGS AND ALEVINS

The concentration of dissolved oxygen in intragravel water in August and September 1965 helped confirm earlier conclusions (McNeil, 1966) that the environment is more favorable for eggs in the upper area than in the middle or lower area. Samples of intragravel water, collected from random points within each area August 16 and 31 and September 13 and 22, were analyzed for dissolved oxygen (table 11).

Dissolved oxygen concentrations of intragravel water were high in August but low in September, when a drought became severe. The low values in September were due partly to consumption of the dissolved oxygen in the stream water by decomposing salmon carcasses. Dead salmon are usually removed from Sashin Creek during freshets, but no freshets occurred in September 1965. The dissolved oxygen cannot be replenished without extensive exposure to the air. The upper area, which has a steep gradient and turbulent water, provided for more rapid replenishment of dissolved oxygen than the calm water in the lower area, which has a shallow gradient. Metabolites that are not freely exchanged with the atmosphere, such as ammoniacal nitrogen, also may have accumulated in the lower area.

TABLE 11.—*Dissolved oxygen content of intragravel water in three areas in Sashin Creek, 1965* [1]

Study area and date	Water temperature	Dissolved oxygen concentration		Degree of saturation
		Mean	90-percent confidence limits of mean	
	° C.	*Mg./l.*	*Mg./l.*	*Percent*
Upper:				
August 16	12	9.7	±0.7	90
August 31	12	9.9	± .7	91
September 13	11	6.2	± .9	56
September 22	12	7.6	± .8	71
Middle:				
August 16	12	8.9	± .8	82
August 31	12	9.7	± .7	90
September 13	11	3.8	± .8	34
September 22	12	4.3	± .6	40
Lower:				
August 16	12	8.5	±1.1	78
August 31	[2] 12	------	------	------
September 13	11	2.3	± .3	20
September 22	12	2.9	± .6	27

[1] Methods of sampling were described by McNeil (1962).

[2] The August 31 samples were collected 1 day after a freshet; the data for the lower area are omitted because 60 percent of the standpipes in the area had been washed away.

I expected to find that the percentage of eggs alive at the end of spawning would be highest in the upper area and lowest in the lower area because of the progressively decreasing amounts of dissolved oxygen in intragravel water downstream. On September 29, 84 percent of total eggs were alive in the upper area; 86 percent in the middle area; and 60 percent in the lower area (table 5). Although the lowest survival of eggs was in the lower area, as anticipated, I was surprised to find survival of eggs in the middle area similar to that in the upper area. The percentages of live eggs did not change significantly in any of the areas between September 29 and November 20 (table 5).

The development of embryos was somewhat retarded in the middle and lower areas. Laboratory experiments have demonstrated that oxygen privation during early development may retard growth and development of embryos without causing death (Silver, Warren, and Doudoroff, 1963; Shumway, Warren, and Doudoroff, 1964). When oxygen is deficient, it is usual for hatching to be delayed. This fact was confirmed in Sashin Creek in 1965 where the percentage of eggs hatching by November 20 was 77 percent in the upper area, 30 percent in the middle, and 11 percent in the lower.

The tendency of late spawners to concentrate in the lower area (table 10) may have contributed to the later hatching there, but it was not a factor in the middle area where the proportion of early and late spawners was the same as in the upper area.[2] Temperature apparently was not a factor either, because repeated measurements of the temperature of intragravel water failed to demonstrate differences among the three areas. I conclude, therefore, that hatching was delayed in the middle area because embryos had been exposed to low concentrations of dissolved oxygen in September. The late hatching in the lower area may have resulted from a combination of later time of egg deposition and exposure to low dissolved oxygen.

DISAPPEARANCE OF EGGS AND ALEVINS FROM SPAWNING BEDS

The disappearance of eggs and alevins of the 1965 brood was characterized by (1) disappearance of relatively few eggs from the upper and middle areas in summer during spawning, (2) disappearance of relatively large numbers from the upper and middle areas in autumn after spawning, and (3) disappearance of many eggs from all three areas in winter.

Fewer eggs disappeared during spawning in 1965 than in 1963 even though the densities of spawners were similar (table 12). In 1963, when the density was about 0.6 female per square meter, 22 percent of the potential egg deposition was estimated to have disappeared during spawning in the upper area, 42 percent in the middle area, and 62 percent in the lower area. In 1965, at similar densities of spawners, much smaller percentages of the potential egg deposition disappeared during spawning: 7 percent in the upper area, 5 percent in the middle area, and 31 percent in the lower area.

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[2] A chi-square comparison of the proportion of early and late spawners in the upper and middle areas (x^2, degree of freedom, $=0.17$) demonstrated that the proportion of early and late spawners was the same in these two areas.

The high percentage of eggs deposited in 1965 may have resulted from low streamflow in the period of spawning. Except for a freshet on August 30, which produced a discharge of 3 m.³ per second, streamflow remained relatively low (less than 1 m.³ per second) throughout the period of spawning. Streamflow did not increase until October 3 (after spawning had ended) when a second freshet produced a flow of 7 m.³ per second.

TABLE 12.—*Percentage of potential egg deposition of pink salmon that disappeared from three areas in Sashin Creek during autumn and winter, 1963 and 1965 brood years*

Area and season	Estimated portion of potential egg deposition disappearing	
	1963 brood	1965 brood
	Percent	*Percent*
Upper:		
Summer (during spawning)	22	7
Autumn (after spawning)	32	24
Winter	2	27
Middle:		
Summer (during spawning)	[1] 42	5
Autumn (after spawning)	0	26
Winter	1	30
Lower:		
Summer (during spawning)	62	31
Autumn (after spawning)	0	0
Winter	0	24

[1] Estimate pertains to the early two-thirds portion of the period of spawning. Other estimates for summer were at the end of spawning.

A relatively high percentage of the potential egg deposition (36 percent) disappeared from the upper area of Sashin Creek after spawning in autumn 1963, but few eggs and alevins disappeared in winter (table 12). Because the pattern of disappearance was dissimilar in the middle and lower areas in 1963, I postulated that scavengers or predators may have concentrated in the coarse bottom materials of the upper area to feed on eggs and alevins (McNeil, 1966). As I will show shortly, however, turbulent water during periods of high discharge in autumn may also have contributed to the disappearance of eggs from the upper area.

The rate of consumption of eggs and alevins by scavengers and predators is not known, but many species of invertebrates are known to inhabit spawning beds where they may feed on eggs and alevins (Briggs, 1953; Ahnell, 1961; McDonald, 1960). Other investigators (McLarney, 1964, and Phillips and Claire, 1966) have found that sculpins (*Cottus* spp.) are capable of penetrating into streambeds and will feed on eggs and alevins where fine particles do not restrict their movements. The population of sculpins in Sashin Creek has been estimated to include 15,000 to 20,000 fish 5 cm. or longer total length (McLarney, 1964). According to McLarney (personal communication), this number of sculpins would be capable of consuming a significant portion (perhaps 25–50 percent) of the total number of eggs estimated to have disappeared in the autumn of 1963 (about 1 million) and the autumn of 1965 (about 2 million).

McLarney (personal communication) also found that many eggs deposited in coarse materials are near the surface of the streambed and are vulnerable to predation and to removal from the bed by water turbulence. He detected the presence of eggs near the surface of the bed by artificially creating water turbulence within a 0.2-m.² circular screen placed on the surface of the bed and collecting the eggs that were released from the streambed. About 150 points were tested in this manner in each of the three areas during spawning in 1965 (about 25 points per area on each of six dates). The number of eggs collected by McLarney per 0.2 m.² in the upper area was 3 times the number in the middle area and 14 times the number in the lower area. Thus, eggs were most susceptible to predation and to removal from the bed by turbulent water in the relatively coarse bed materials of the upper area and least susceptible in the relatively fine materials of the lower area. This result helps to explain why no eggs disappeared from the lower area in the autumns of 1963 and 1965 (table 12).

Other studies have shown that the portion of eggs and alevins that disappear from Sashin Creek spawning beds varies from winter to winter. The number of eggs and alevins did not decrease during the winters 1961–62 and 1963–64 (McNeil et al., 1964; McNeil, 1966); yet in the winter of 1965–66, an estimated 27 percent of potential egg deposition disappeared from spawning beds of Sashin Creek. Factors causing the disappearance of eggs and alevins in the winter of 1965–66 have not been identified.

SEASONAL VARIATION IN MORTALITY IN SPAWNING BEDS

The number of live pink salmon eggs of the 1965 brood declined from an estimated 12.7 million at the beginning of spawning in summer to 8.3 million at the end. Mortality caused further reductions to 6.5 million in autumn and to 2.2 million in winter.

It is instructive to compare mortality of the 1965 brood with that of the 1963 brood. For this comparison, I have calculated values of the mortality coefficient, M, for the entire stream rather than for the individual areas as given in table 8 of this paper and in table 11 of McNeil (1966). The values for M for brood years 1963 and 1965 for period 1 (summer), period 2 (autumn), and period 3 (winter) are as follows:

Brood year	Summer	Autumn	Winter
1963	0. 76	0. 11	0. 07
1965	. 31	. 15	. 26

Although the rate of mortality both years was highest during spawning, the difference between the two years was appreciable (2½ times). Mortality in autumn was similar for the two years, but the difference between the years was pronounced in winter (3½ times). Differences in mortality coefficients are suggestive of differences in the environment encountered by the two populations, because the number of spawners was similar each year (16,757 in 1963 and 14,833 in 1965). The unusual drought which prevailed throughout September 1965 could have produced increased survival during spawning from increased efficiency of egg deposition in spawning beds and decreased survival in autumn and winter from delayed mortality of embryos and alevins exposed to low concentrations of dissolved oxygen early in development.

SUMMARY

1. The area of streambed in Sashin Creek used by pink salmon for spawning is 13,629 m.^{2} Observations on distribution of spawners and survival of embryos and alevins are made annually in 97 percent of the spawning ground which is divided into upper (2,945 m.^{2}), middle (4,067 m.^{2}), and lower (6,072 m.^{2}) areas.

2. Migration of 14,833 pink salmon spawners to Sashin Creek in 1965 was relatively early, and high fresh-water survival of their progeny (18 percent of potential egg deposition) resulted in the production of 2,235,000 fry. High survival was predicted at the time the parents entered the stream from a linear relation of survival of progeny and the date the parents entered the stream.

3. Although the density of spawners was relatively high and fairly uniform throughout the stream, densities of fry were considerably different in the upper, middle, and lower areas. The highest density of fry (228 per square meter) was in the upper area; the lowest (104 per square meter) was in the lower area. The relatively high density of fry in the upper area and low density in the lower area resembled the situation in three previous years (1959, 1961, and 1963) when the density of spawners in the three areas was also relatively high.

4. Spawners do not concentrate in the upper area despite the existence of a favorable environment for embryos and alevins. Failure to concentrate in that area is most pronounced when spawners are scarce, but the reasons for this behavior remain obscure.

5. Delayed hatching of eggs in the autumn of 1965 was attributed to low dissolved oxygen in intragravel water, which resulted from a drought throughout September. Detrimental effects of the drought on embryos were least pronounced in the upper area where concentrations of dissolved oxygen in intragravel water were highest.

6. Rates of disappearance of eggs and alevins from spawning beds in 1965–66 were low during spawning and high during winter in comparison with previous years. Low waterflow in September 1965 may have allowed a better than normal recruitment of eggs to spawning beds. The disappearance of large numbers of eggs and alevins in winter is unexplained.

7. The rate of mortality of the 1965 brood year was two times higher during spawning than in autumn. This situation is contrasted with the 1963 brood, whose rate of mortality was about 7 times higher during spawning than in autumn and about 11 times higher than in winter.

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PRELIMINARY ANALYSIS OF THE CATCH CURVE OF THE PACIFIC SARDINE, *Sardinops caerulea* Girard

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ABSTRACT

This is a report on a method of estimating age-dependent changes in rates of natural mortality and the age- and season-dependent changes in rates of availability of the Pacific sardine. It includes estimates of the virtual average catch curve and relative year class strengths and deviations of individual curves from these estimates. The calculations are carried out with each of three sets of data: total California catch, catch per unit of effort in central California, and catch per unit of effort in southern California.

The average catch curve allows an estimate to be made of the increase in the natural mortality rate during fully recruited ages. The deviations of individual curves are assumed to represent the annual changes in rate of availability of each year class under a certain condition. The deviations of different age groups in the same years are compared to give a general idea of age-dependent change in the rate of availability in a year. Availability is also examined in regard to ocean temperatures preceding the fishing season.

A detailed model is proposed to estimate parameters relevant to the sardine population on the basis of the above examination as well as on the basis of earlier estimates of rates of natural mortality and availability. Consideration of the detailed model indicates the necessity for several sources of information to establish methods for predicting the sardine catch.

A fisherman's income depends on the size and behavior of stocks of fish entering his fishing grounds as well as on the efficiency of his gear. A fishery biologist must predict the size of the fish stocks available to the commercial fisheries. Taylor's[2] multiple regression equation, based on temperature and salinity in the year of spawning and on body length at the end of the first year of life, predicts the virtual stock size of a Pacific sardine year class. Availability of this fish, however, varies from season to season (Widrig, 1954), thus complicating the problem of prediction. To be useful to the fishermen, therefore, forecasts are needed for particular seasons and they must be based on yearly changes in availability in addition to year-class strength.

Widrig (1954) used relative rate of availability of the Pacific sardine to estimate population sizes and Yamanaka[3] developed a method for estimating the absolute value of the rate. Both authors started from the formula:

$$Z=M-\log\{re^{-fQ}+(1-r)\} \qquad (1)$$

where Z and M denote instantaneous coefficients of total and natural mortalities as defined by Holt, Gulland, Taylor, and Kurita (1959). Other symbols are defined as: f=amount of effort, Q=efficiency of unit effort, and r=rate of availability.

Widrig (1954) and Yamanaka[3] assumed that the rates of natural mortality and availability are constant for four age groups (III- to VI-year-old fish). Introducing age-dependent changes in these rates into the calculations complicates the problem. Because the above authors did not do so, it is necessary to check the assumptions of equation (1) from another point of view.

In this paper I am interested in three matters. First I determine, through a simple examination of the catch data, if there is evidence of age-dependent changes in natural mortality and in availability. I also compare the various estimates of availability and their relation to an environmental factor, ocean temperature. Then I present a method to estimate the parameters on more probable assumptions resulting from these examinations.

GENERAL STATEMENT

In the first examination of the age data, I made

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[1] This manuscript was prepared during the author's visit at the Bureau of Commercial Fisheries Biological Laboratory, La Jolla, Calif., November 1959 to October 1960.

[2] Taylor, Clyde C. Some factors associated with year class size of the Pacific sardine. Bureau of Commercial Fisheries Biological Laboratory, La Jolla, Calif. (Manuscript).

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no attempt to estimate the absolute value of rate of availability, but rather I estimated the fluctuations in it as related to season and age. Strictly speaking, availability should be divided into two categories: (a) accessibility, the fish stock (in terms of numbers) accessible within the range of the fishermen and (b) vulnerability, which depends on factors involving gear efficiency. Measuring vulnerability in the commercial catch requires more than the examination of age composition and the amount of effort. I comment on this problem later. In the absence of information to separate availability into its components, their separate effects are disregarded here and included in the changes in availability and mortality.

Two basic assumptions are requisite for the first study of the relation of fluctuations to season and age: first, that the total mortality coefficient fluctuates randomly around a mean; and second, that the rate of availability fluctuates around a logarithmic mean. Even though no fishery may satisfy these assumptions, they may be accepted for a first approximation when age and year class are significant sources of variation in catch compared to the interaction that is a measure of total effects of changes in rates of mortality and availability as well as survey errors. In other words, changes in mortality and availability are regarded as less important in determining the catch than age and year-class strength when the latter two are significant sources of variations.

FORMULATIONS

Without exception the number of the *i*th year class caught in the year when they were *j*th age, C_{ij}, is expressed as:

$$C_{ij}=N_{io}\cdot r_{ij}\cdot E_{ij}\cdot \prod_{a=0}^{j-1}\cdot S_{ij}=N'_{io}\cdot r_{ij}\cdot E_{ij}\cdot \prod_{a=tp}^{j-1}\cdot S_{ia} \tag{2}$$

where: S_{ij}=annual rate of survival of the *i*th year class at *j*th age, E_{ij}=rate of exploitation for the available part of the *i*th year class at *j*th age, tp=youngest age in maturing spawning products, N_{io}=initial stock size of the *i*th year class, N'_{io}=stock size of the *i*th year class at the beginning of the year when they were tp year (s) old.

Under conditions assumed above, it holds that

$$\log C_j=\log N'_o-\sum_{a=t_p}^{j-1} Z_a+\log r_j+\log E_j \tag{3}$$

where, $\log C_j$=logarithmic average of all catches of *j*th age fish over year classes, $\log N_o$=logarithmic average of recruitment stock sizes over year classes, Z_a=average mortality coefficient at *a*th age over year classes, $\log r_j$=logarithmic average of availability rates at *j*th age over year classes, $\log E_j$=logarithmic average of exploitation rates at *j*th age over year classes
and

$$\log C_{j+1}=\log N'_a-\sum_{a=t_p}^{j} Z_a+\log r_{j+1}+\log E_{j+1} \tag{3'}$$

and then

$$\log C_{j+1}-\log C_j=-Z_j+(\log r_{j+1}-\log r_j)+(\log E_{j+1}-\log E_j) \tag{4}$$

If *j*th age fish migrate with fish older by 1 year, formula (4) approaches $-Z_j$ for data available over a period of years, if there is no trend in the rates of exploitation and availability, or if the number of years is large. Thus, the logarithmic means of several ages of fish give a "standard virtual catch curve" for a given period under the above conditions. The standard curve becomes more reliable in estimates of $-Z_j$ as the period under consideration becomes longer and the catch curve of each year class becomes more stable.

Year-class means of $\log C_{ij}$, $\log C_i$, are

$$\log C_i=\log N'_{io}-\sum_{a=t_p}^{t_1} k_a Z_{ia}+\log r_i+\log E_i \tag{5}$$

where $k_a=(t_1-a+1)/(t_1-t_p+1)$, and t_1=the oldest age in question. The last two terms are the year-class means of the logarithms of rates of availability and exploitation, respectively.

These means may not give a good estimate of year-class strength in the sardine because its life span is too short to allow changes in rates of availability and exploitation to cancel each other. It may be regarded, however, as a measure of the mean available stock size of each year class when the year class is found to be a significant source of variation.

Since the logarithmic mean of catches is

$$\log C=\log N'_o-\sum_{a=t_p}^{t_1} k_a Z_a+\log r+\log E \tag{6}$$

we can construct an "expected catch," E ($\log C_{ij}$), when $Z_{ia}=Z_a$ is common for the entire year class and $r_{ia}=r_i$ and $E_{ia}=E_i$ are common for all the age groups of any year class.

$$\begin{aligned}E(\log C_{ij})&=\log C_i+\log C_j-\log C\\&=\log N'_{io}-\left\{\left(\sum_{a=t_p}^{j-1} Z_a\right.\right.\\&\qquad\left.\left.+\sum_{a=t_p}^{j-1} k_a Z_{ia}-\sum_{a=t_p}^{t_1} k_a Z_a\right)\right\}\\&\qquad+(\log r_i+\log r_j-\log r)\\&\qquad\quad+(\log E_i+\log E_j-\log E)\end{aligned} \tag{7}$$

Therefore,

$$\begin{aligned}\Delta_{ij}&=\log C_{ij}-E\,(\log C_{ij})\\&=-\left\{\sum_{a=t_p}^{j-1} Z_{ia}-\left(\sum_{a=t_p}^{j-1} Z_a+\sum_{a=t_p}^{t_1} k_a Z_{ia}-\sum_{a=t_p}^{t_1} k_a Z_a\right)\right\}\\&\quad+\{\log r_{ij}-(\log r_i+\log r_j-\log r)\}+\{\log E_{ij}\\&\qquad-(\log E_i+\log E_j-\log E)\}\end{aligned}\qquad(8)$$

Among the variables in formula (8), we can determine combined effects of yearly changes in mortality coefficients and availability rate. Because $\Sigma_j\Delta_{ij}=0$, the deviations of the same year class should be negatively correlated when the changes in rates of availability and exploitation are less important than change in mortality coefficients in determining the catch curves. On the other hand, significant positive correlation between deviations of any two age groups taken in the same seasons indicates that deviations in availability and exploitation are important.

A similar meaning attaches to any measure that is proportional to the available stock size, such as catch per unit of effort; here the change in rate of exploitation is disregarded. It should be noted that the deviations are affected by the year-class average of logarithms of availability and are not, then, a measure of relative availability on the same base.

TOTAL CALIFORNIA CATCH

Age composition of the California sardine has been reported for 26 seasons, 1932–33 through 1957–58 by Eckles (1954), Wolf (1961), Felin and Phillips (1948), Mosher, Felin, and Phillips (1949), Felin, Phillips, and Daugherty (1949), Felin, Daugherty, and Pinkas (1950, 1951), Felin, Anas, Daugherty, and Pinkas (1952), Felin, MacGregor, Daugherty, and Miller (1953, 1954, 1955), Felin, Wolf, Daugherty, and Miller (1958), Wolf, MacGregor, Daugherty, and Miller (1958), and Daugherty and Wolf (1960). When catch is plotted against age on a semilog scale for each year class, the catch curves are fairly smooth for fish older than age II of most year classes, but are very irregular for some year classes—especially those spawned in 1947 through 1949 (fig. 1). These irregular curves may be due to changes in availability and exploitation. The catch curves of some year classes indicate moderate irregularity. For instance, year classes 1930 through 1933 might have been highly available in the 1936–37 season.

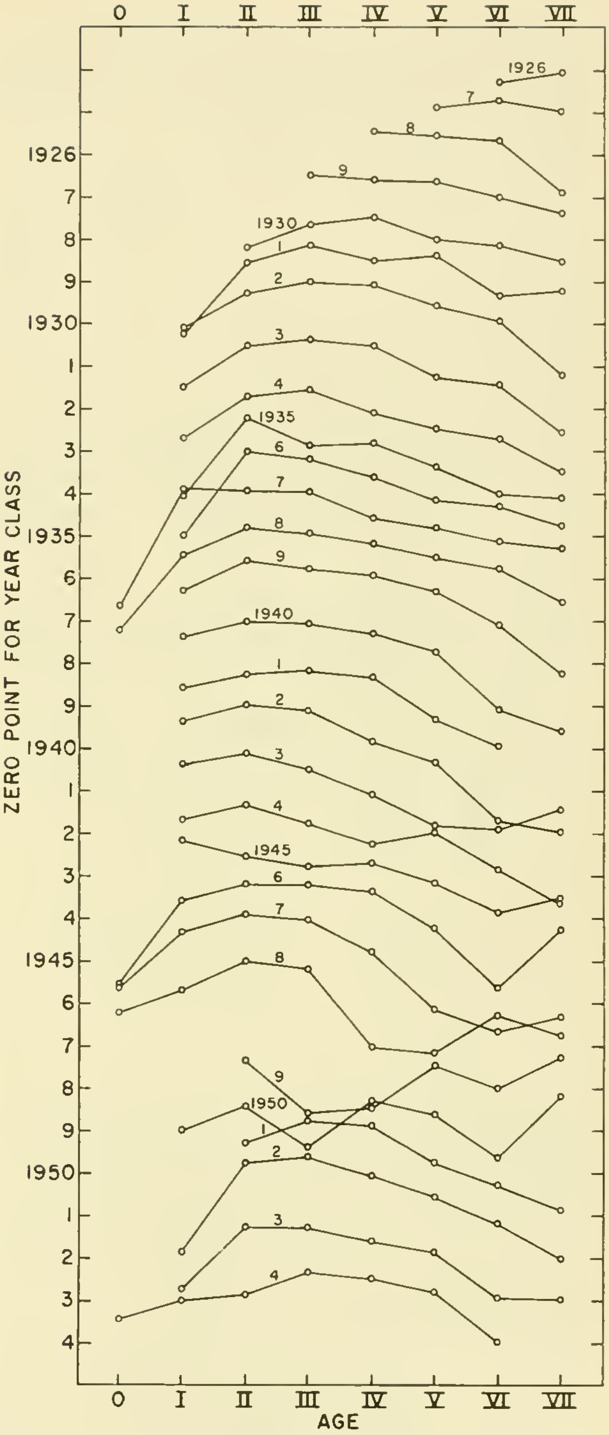

FIGURE 1.—Catch curves of Pacific sardine, year classes 1926 through 1954. Vertical scale equals log of millions of fish; distance between zero points for each year class equals 1.0 (i.e., 10,000,000 fish).

The age- and year-class mean of log C_{ij} for the 22 year classes from 1930 to 1951 are, nevertheless, regarded as sufficiently significant to give a reliable standard catch curve and estimates of year-class strength of the available stocks. Analysis of variance of the means of logarithms of the total sardine catch in California for the year classes 1930 through 1951 gives the following:

Source of variation	Degrees of freedom	Mean square
Age	4	*6.1756
Year class	21	*1.3825
Residual	84	.2851

*Significant at a probability of less than 0.1 percent.

The average catches by age indicate that sardines are not fully recruited until age III (table 1). The increase in the mortality coefficient, even after age III, may be attributed partly to incomplete recruitment after this age and partly to an increase in natural mortality.

Table 1.—*Mean sardine catch (ln), total mortality coefficients, and change in mortality by age for the year classes 1930–51 and 1930–44 in California*

Age (j)	Mean catch (ln)		Mortality coefficient (Z_j)		$Z_{j+1}-Z_j$	
	1930–51	1930–44	1930–51	1930–44	1930–51	1930–44
	Millions of fish	*Millions of fish*				
II	310.0	646.7				
			−0.09	0.11		
III	340.9	579.9			0.72	0.60
			.63	.71		
IV	176.5	284.0			.32	.28
			.95	1.00		
V	65.1	104.9			.24	.23
			1.19	1.23		
VI	18.8	30.6				

Because of incomplete records, the expected catches of eight year classes, 1926–29 and 1951–57, are constructed through their mean catches and a standard catch curve, so that $\Sigma_j \Delta_{ij}$ reduced to zero. When these additional classes are included, the deviations of logarithmic catches of any two age groups in the same season are positively correlated with each other, where the effects of environment and fishing intensity might be expected to be common for all the age groups. The correlation coefficient is higher for combinations of adjacent age groups (fig. 2). On the other hand, correlation coefficients between deviations in two ages from the same year classes range from −0.690 to 0.307. This variability indicates that change in survival rate is less important than change in availability and exploitation.

From these observations in regard to assumptions given in the last two paragraphs of the preceding section (on formulations), it may be assumed that the year-class-dependent change in total mortality coefficients is smaller than the seasonal changes in both availability and exploitation and that the migratory pattern differs from age to age but is similar for adjacent ages. The multiple correlation of deviations of age groups III to V in the same season was calculated to be as high as 0.815. These three age groups furnished the greater part of the period under discussion.

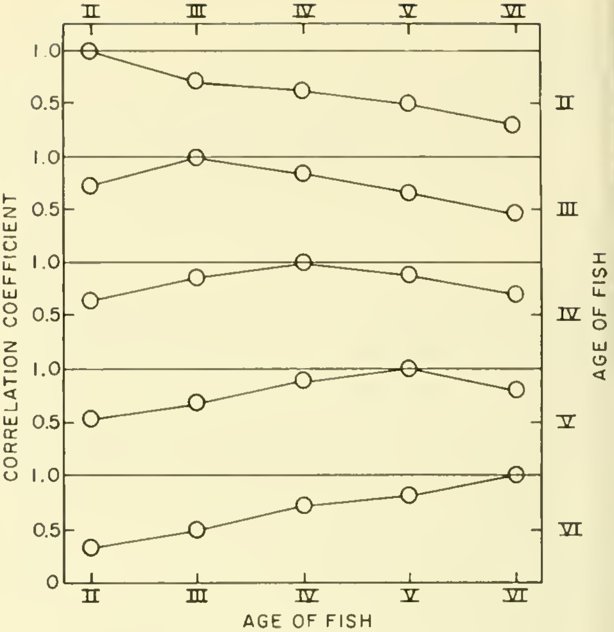

Figure 2.—Correlation coefficients between index of virtual availability of two age groups, based on the total catch in California, 1932–33 through 1957–58 seasons.

It is well known that the migratory pattern of the Japanese sardine and its fishing grounds are affected by changes in oceanographic conditions (Sako, 1939; Shimomura, 1954). Because sufficient information about the environment of the fishing grounds in California waters was lacking, I correlated the temperature anomaly at the pier of the Scripps Institution of Oceanography for July through September (just before the fishing season) with annual mean deviations in the catch of the three major age groups for 26 seasons (fig. 3). The correlation coefficient was 0.599, slightly over the 1-percent level of significance.

Clark and Daugherty (1950) reported the catch per unit of effort and total effort of the purse seiners in California waters as well as at each of the three major ports, San Francisco, Monterey, and San Pedro, for the seasons 1932–33 through 1948–49. To eliminate the effects of improvement

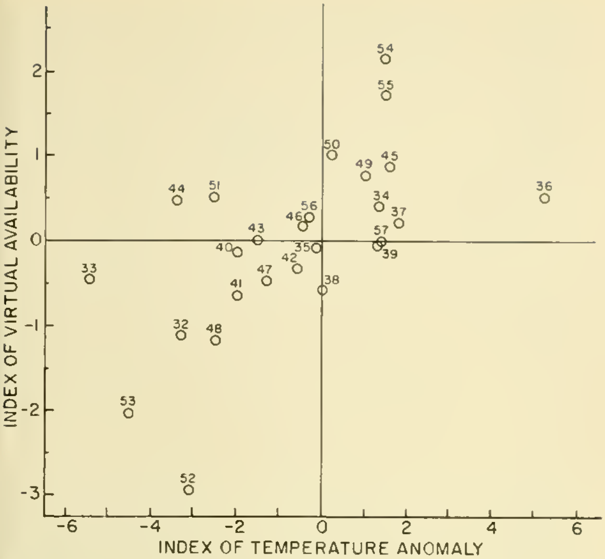

FIGURE 3.—Relation between temperature anomaly at pier of the Scripps Institution of Oceanography and virtual availability of sardines in California, 1932–33 through 1957–58 seasons. Numerals denote the fishing season, e.g., 32 indicates the season of 1932–33.

in the efficiency of individual boats, they adjusted the catch per unit of effort using as base year the 1932–33 season at each port. The same authors (1952) reported the data for the 1949–50 and 1950–51 seasons in all California waters, as well as at Monterey and San Pedro, and Clark (1956) published the data for the four seasons 1951–52 through 1954–55 in southern California. In the latter two works the authors chose the 1941–42 season as the new base year (Clark and Daugherty, 1950) to fit recent developments in the fishery.

Because fishing effort should be expressed on the same base year, I converted the catch per unit of effort in the whole fishing season to the value based on that of the 1941–42 season. Since the fishing grounds off California are divided into two regions of almost equal area, the north off San Francisco and Monterey and the south off San Pedro (Widrig, 1954), the total effective effort is calculated by dividing the total California catch by the sum of catches per unit effort in the two regions. The deviations of catch showed a significant multiple correlation coefficient of 0.594 with the temperature anomaly and the amount of fishing effort. Partial correlation coefficients were 0.293 for fishing effort and 0.585 for temperature anomalies.

CATCH PER UNIT OF EFFORT

Because fishing effort appeared to show a positive correlation with the deviation of catch from the expected value, I repeated the above calculations for total catch, using the catch per unit of effort. Present evidence indicates that the stock exploited in the waters off central California is mainly composed of fish spawned in the waters off southern California (northern subpopulation), whereas the stock in southern California includes fish spawned off central Baja California (southern subpopulation) as well as fish from the northern subpopulation (Felin, 1954; Marr, 1960). The effort data are not given after the 1951–52 season for central California where the fishery practically disappeared by 1954. Catch per unit of effort at San Francisco, Monterey, and San Pedro indicates that the available stocks off the two northern ports are correlated with a significant coefficient of 0.810 but that the stock off San Pedro is not correlated with either San Francisco (0.314) or Monterey (0.398) during the 19 seasons from 1932–33 to 1950–51. This lack of correlation may be attributed to differences in the subpopulation supporting the fisheries. It is also possible that the northern subpopulation, having migrated to central California, left only a minor portion of the stock in southern California or that major age groups differed between these regions.

Since it is desirable to forecast regional catches, the following discussion is based on data by region. In the northern waters the catch curves for ages II to VI, based on catch per unit of effort, were obtained for the 1930–44 year classes. The curves were fairly regular for most of the year classes, except the last. The following table shows that age and year class are significant sources of variation of logarithmic catch, as was true for total catch:

Source of variation	Degree of freedom	Mean square
Age	4	*4.4487
Year class	14	*1.2050
Residual	56	.1596

*Significant at a probability of less than 0.1 percent.

The following tabulation of the standard catch curve based on logarithmic means of the catch per unit of effort in central California for the year classes 1930–44 shows that there is less change in mortality rate with age than was found for total catch (table 1):

Age (j)	Mean catch (thousands of fish)	Mortality coefficient (Z_j)
II	656.6	
III	592.5	0.10
IV	264.7	.81
V	102.5	.95
VI	33.7	1.11

The deviations from the expected catch for some year classes did not always indicate significant negative correlation; the coefficients range between −0.661 and 0.478. On the other hand, the deviations in the same season were always positively correlated; the coefficients vary between 0.280 and 0.850. It is again found that the closer the ages, the higher the correlation coefficients. The multiple correlation coefficient for the three major age groups is 0.877.

In the southern California catch, the curves were irregular for the year classes that occurred after 1947. The following analysis of variance of the means of logarithms of the catch per unit of effort in southern California for the year classes 1930–48 shows that age and year class are significant sources of variation:

Source of variation	Degrees of freedom	Mean square
Age	4	*1.6133
Year class	18	*2.0954
Residual	72	.1244

*Significant at a probability of less than 0.1 percent.

The standard catch curve is fairly smooth after age III; age-dependent changes in mortality are minor. The four year classes that were produced in 1945–48, however, may differ in survival rate as well as in stock size (table 2). The correlation coefficient between deviations of the same year class fluctuates broadly between −0.495 and 0.138. The correlations between deviations in the same season are always positive, 0.223 to 0.890, and are higher for two adjacent age groups; the multiple correlation coefficient for age groups III to V was as high as 0.910.

The mean deviations for age groups III through V in central and southern California fluctuate similarly; the correlation coefficient between them was 0.810. Compared with the different regional fluctuations in catch per unit of effort of all the age groups, this similarity may suggest that some younger and older age groups than those in question showed different changes in availability between these two regions.

Table 2.—*Mean sardine catch (ln), total mortality coefficients, and change in mortality by age for the year classes 1930–48 and 1930–44 in southern California*

Age (j)	Mean catch (ln)		Mortality coefficient (Z_j)		$Z_{j+1}-Z_j$	
	1930–48	1930–44	1930–48	1930–44	1930–48	1930–44
	Millions of fish	*Millions of fish*				
II	907.6	888.5				
			0.26	0.27		
III	701.9	680.2			0.77	0.61
			1.03	.87		
IV	251.1	283.6			.24	.33
			1.26	1.20		
V	71.1	85.2			.07	.29
			1.33	1.49		
VI	18.8	14.3				

The temperature anomaly at Scripps pier does not correlate well with the deviations in catch, but is slightly higher with those in central California (0.560) than with those in southern California (0.495).

DYNAMICS OF THE PACIFIC SARDINE FISHERY

This discussion deals with the age-dependent changes in rates of natural mortality and availability derived from information obtained thus far. A detailed model is presented for estimating the parameters inherent in the population dynamics of the Pacific sardine.

All three sets of data analyzed above indicate three characters of catch curves of the sardine: (a) the increase of the virtual total mortality coefficient with age; (b) the close relation between virtual indices of availability of two adjacent age groups; and (c) the dependence of the availability on temperature in the months just before the fishing season. To examine the reliability of these findings, similar analyses are repeated with estimates of these parameters as presented by Widrig (1954) and Yamanaka (footnote 3).

Previous authors assumed that the natural mortality coefficient was constant over the four age groups III through VI. In Widrig's study (1954) three appropriate values of the coefficients were assumed, and the rate of availability in a season was shown in relative rate to that of the 1936–37 season for each of these assumed coefficients. Yamanaka (footnote 3) assumed that the natural mortality coefficient fluctuated around a mean and that the rate of availability fluctuated around a logarithmic mean for the 23 seasons from 1932–33 to 1954–55. Because the level of availability changed between the early and later years of the investigation, he divided the period into two parts; one from 1932–33 to 1945–46, and the other from 1945–46 to 1954–55. The present report examines only his final estimates based on the divided data. Because these authors first estimated the rate of availability in logarithms, my analysis of the rate is usually made with logarithmic rather than actual values.

As estimated by Yamanaka (footnote 3), the increase in virtual total mortality coefficients with age is comparable to decrease in availability of older fish. As expected from his assumption, availability should decrease with age if total mortality increases. Therefore, I conclude that the virtual coefficient of total mortality of the Pacific sardine increased with age for the period investigated.

The age-dependent change in the virtual coefficient of total mortality may be partly attributed to incomplete recruitment [4] in addition to a real change in natural mortality, insofar as it is estimated from the age composition of the commercial catch. Although no conclusive evidence is obtained, it seems to me that the increase in natural mortality with age is real rather than caused by incomplete recruitment for the fish at and older than the three ages discussed, since the fishery has exploited fish as young as age I and sometimes age zero. If this increase in natural mortality with age is real, the natural mortality coefficient of these fish is considered to increase linearly with age (table 1). A linear increase of the coefficient with age was postulated by Beverton and Holt (1957, pp. 69–71) for three species: two herrings, *Clupea harengus harengus* and *C. harengus pallasi*, investigated by Hodgson (1932) and Tester (unpublished, cited by Ricker, 1948) and the whitefish, *Coregonus clupeaformis*, of Lake Opeongo studied by Ricker (1949). A linear increase with age may not always hold, however, as was shown for the same species, or ecologically related ones, surveyed on other occasions: namely the whitefish of Shakespeare Island Lake, the sauger, *Stizostedion canadense*, of Lake Opeongo (Ricker, 1949), and the herring, *C. harengus pallasi* (Tester, 1955).

It is noteworthy that total mortality coefficients are higher in southern California than in central California—also the increments, which average about 0.30 in southern California but 0.15 in central California, as previously shown. This difference is partly attributed to differential distribution of the fish by age; older fish migrate farther north. It should be noted, however, that Yamanaka (footnote 3) estimated the natural mortality coefficient of the sardines to be higher in the more recent years, when the southern subpopulation predominated, than in earlier years for the entire range of the fishery in California. Thus, both his and my results agree that the mortality rate is higher in the southern subpopulation than in the northern one.

It has been shown thus far that the rate of availability differed between age groups exploited in the same fishing season but that it was close for two adjacent age groups. A comparable result is obtained from the analysis of the availability rates as estimated by Yamanaka (footnote 3). As to the age-dependent change in availability, it has already been suggested that some species of fish school together by size or by age, including, among others, the herring, *C. harengus* (Hjort, 1926, p. 8); the sardine, *Sardinops melanosticta* (Yamanaka, 1955, p. 51); the anchovies, *Engraulis mordax* (Miller, 1955, p. 30), and *Cetengraulis mysticetus* (Howard and Landa, 1958, p. 394); the yellowfin tuna, *Thunnus albacares* (Schaefer, 1948, p. 199); and the skipjack tuna, *Katsuwonus pelamis* (Brock, 1954, p. 99).

As an approach to predicting catch, the temperature data at Scripps pier just before the fishing season were regarded as having been correlated with the preliminary estimates of availability. The correlation coefficients between temperatures and the logarithms of each series of estimates by Widrig (1954), based on assumed values of the natural mortality coefficients of 0, 0.2, and 0.4, are 0.256, 0.305, and 0.300, respectively. Since Yamanaka (footnote 3) estimated the natural mortality coefficient to be 0.35 for all the seasons, or 0.25 for 1932–33 through 1945–46 and 0.65 for 1945–46 through 1954–55, the most probable rate of Widrig's estimates of availability, based on the assumed natural mortality coefficient of 0.4, is best correlated with temperature. In Yamanaka's estimates, the correlation coefficient with temperature is 0.686—higher than that calculated by me or by Widrig (1954).

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[4] Age of complete recruitment of a partially available population is defined as the age at which all the fish are potentially "catchable" by the fishery even if, actually, some of them do not always enter the fishing ground. When rates of availability are estimated for all the age groups appearing in the catch, the age of complete recruitment is determined by comparison of the average rate for each age.

The correlation coefficient based on the rate of availability is 0.757 and, thus, higher than that based on the logarithmic values.

Summarizing these examinations of the age composition of the sardine catch by Widrig (1954), Yamanaka (footnote 3) and the present study, I may be able to assume the following characteristics of the available sardine stocks:

a. The natural mortality differs by age and by subpopulation and probably by year class; therefore, I recommend that the rate be estimated for each age group with the data taken in the shortest period of years for which the analysis can be made and for each fishing ground in which the stock is more homogeneous.

b. The availability also differs by age of the fish. It is indicated, however, that the rates of two successive age groups are similar. This fact also indicates that the parameters should be estimated for each age group separately.

c. Availability seems to be correlated with temperature. This possibility should be studied in relation to temporal and areal patterns of the environment, as well as the general levels of availability. For instance, Craig (1960) demonstrated that the herring catch was related to increase in temperature and strength and direction of winds in early summer, even though the catch was not highly correlated with each of these factors. Factors such as these, regarded important in Japan, include temperature distribution, intensity of cold water masses (upwelling), and current strength and direction (Shimomura, 1954).

A more detailed model is presented on the basis of age specific mortality and availability characteristics. Because rates of availability of two adjacent age groups in any year may be assumed to be almost the same, the virtual survival rate, S'_{at}, obtained from age and catch data is expressed as:

$$\begin{aligned} S'_{at}&=\exp(Z'_{at})=(N_{a+1\cdot t+1})/(N_{at}r_{at}) \\ &=\{r_{at}e^{-f_tQ_{at}}+(1-r_{at})\}e^{M_{at}}r_{a+1\cdot t+1}/r_{at} \qquad (9) \end{aligned}$$

then

$$\begin{aligned} Z'_{at}=M_{at}-\log\{r_{at}e^{-f_tQ_{at}}+(1-r_{at})\} \\ +(\log r_{at}-\log r_{a+1\cdot t+1}) \qquad (9') \end{aligned}$$

where a and t denote age of fish and season, respectively. It is assumed that r_{at} and Q_{at} are equal to $r_{a\cdot t+1}$ and $Q_{a\cdot t+1}$ respectively.

The mean of virtual mortality coefficients for n seasons is the sum of means of the first and second terms, and $(\log r_{a\cdot 1}-\log r_{a\cdot n+1})/n$. Then, if Q remains constant for a long period of years so that the last term diminishes to zero, the means of the parameters including Q, M, and r are estimated as shown by Yamanaka (footnote 3). The value of Q, however, should be regarded as variable during rather short periods of years, partly depending on gear improvement, such as the several gear improvements in the sardine fishery in California. In addition, Q may vary because of biological and economic reasons even if the same type of fishing gear is used. The major factors relating to this quantity may be classified in the following three groups:

a. The first and most essential factor affecting Q depends on such variables as fish size, gear type, and speed of hauling. This factor and the mechanical selectivity discussed below, defined as q in the following discussion, determined the efficiency of a fishery for a particular size of fish distributed in a certain way.

b. The second factor, selectivity, is related to both the fish and the fishery. Two general categories of selectivity should be distinguished. The first is a mechanical selectivity, such as the size and number of fish retained by the gear, and is determined by the relation between sizes of mesh or hook and fish; the second is an economic selectivity, controlled by market performance by size or species. The former type of selectivity is included in the first category (a above) of factors controlling Q. The mean of the latter selectivity factor is included in the rates of natural mortality. The deviation from mean is included in availability.

c. The third factor, volume of the water in which the available part of the stock is distributed, also causes change in Q even though the rate of availability is constant. The same gear should be more effective or the same fishermen should locate the schools more readily when the fish are distributed in smaller volumes of water than in larger ones. Changes in patchiness and depth of distribution may not be as important as the size of the waters when the discussion concerns a whole season during which total effects may be nearly constant. Since sardines may remain in a particular stratum, the volume of water may be approximated by the area of fishing ground, A, that is measured by location of the hauls or isothermal contours.

The first approach regards the value of Q as q/A. Since catch per unit of effort is related to the mean density of the fish stock in the fishing ground, as well as to the efficiency of individual gear, this quantity should be adjusted by an appropriate measure (such as area of fishing ground) to yield the relative stock size and the virtual mortality coefficient (Gulland, 1955; Beverton and Holt, 1957). Watt (1956, p. 629) pointed out that the catch per unit of effort, obtained by dividing the total catch by total effort in a season, is not realistic when availability changes within the season. He, therefore, compared the stock sizes in 2 years by the catch per unit of effort in a particular month.

If a fishery is operated in several localities, there is no reason to believe that rate of availability (accessibility and vulnerability) is common for the total range of the fishery. Each locality should be studied, especially if the stocks in different areas are composed of different subpopulations.

Such studies require that the calculations be carried on for shorter periods and over smaller areas. Because the mean of the last term of equation (9) does not reduce to zero for such a situation, we have to assume the following:

a. M and q fluctuate around their means at random, and their variances are so small that these quantities may be regarded as constant.

b. There is a mean of r that gives a mean of the second term for any given set of q, f, and A.

c. The ratio of availabilities in 2 adjacent years fluctuates around a logarithmic mean at random.

d. The availability and gear efficiency are common for two adjacent age groups.

On the basis of these assumptions, the virtual mortality coefficient of a certain age group of fish during the tth season, $Z'_{t'}$ in an area is

$$Z'_{t'}=M_t-\log\{r_t\cdot\exp(-f_tq_t/A_t)+(1-r_t)\}+(\log r_t-\log r_{t-1}) \quad (10)$$

and the mean of the virtual mortality coefficients of the age group, Z', is

$$Z'=M-\log\{\tilde{r}\exp(-f\tilde{q}/A)+(1-\tilde{r})\}+d \quad (11)$$

where $\tilde{r}$ and $\tilde{q}$ are estimated averages of r and q in the age group, which give the mean of the second term in the formula (10) for a given set of f and A, and $d=\log(r_1/r_0)/m-1$.

The parameters, M, $\tilde{q}$, $\tilde{r}$, and d, may be estimated by the least-squares method if appropriate data which were taken in at least 6 successive years and a suitable computer are available to make the calculations.

Putting $a_t=\exp(-f_t\tilde{q}/A_t)$, and $b_t=\log\tilde{r}a_t+(1-\tilde{r})+d$, the expected virtual mortality coefficient, $E(Z'_t)$, equals $M-b_t$. The differences between observed and expected mortality coefficients, Δ's, are:

$$\begin{aligned}
\Delta_1&=\log\{a_1r_1+(1-r_1)\}+(\log r_1-\log r_2)-b_1,\\
\Delta_2&=\log\{a_2r_2+(1-r_2)\}-(\log r_2-\log r_3)-b_2,\\
&\cdot \qquad\qquad \cdot \qquad\qquad \cdot\\
&\cdot \qquad\qquad \cdot \qquad\qquad \cdot\\
\Delta_5&=\log\{a_5r_5+(1-r_5)\}-(\log r_5-\log r_1+5d)-b_5
\end{aligned} \quad (12)$$

These equations give the rates of availability for these 5 years. Repeating this procedure for each successive 6-year period, we may obtain the running averages of the parameters on which a more advanced discussion can be made. When A is not accurately measured, the calculation of availability, based on the constant $Q=q/A$, may give some clues for estimating vulnerability. When fish show differential distribution by age, the mortality rate in the entire population may be estimated from the summation of the stock size of each age group in each locality. Before calculation, division of the area should be reexamined, such as by areal variation in fishing season and relative size of subpopulations (perhaps by scale characters as well as serological research).

Finally, it should be noted that this type of analysis does not provide absolute values of availability for a whole population. Estimates may differ from each other for availability of an age group in a season by six different series. If relative values of the estimated rates for successive seasons are comparable for all of the six series, however, the absolute rate may be surmised from information on the distribution of stocks and independent from fisheries, such as an egg census. As a matter of fact, estimates of availability rates in this type of analysis could be compared with geographic distributions of egg stocks. This comparison is based on the fact that the distribution of the parent stock of the Pacific sardine was represented by egg distribution for the 5 years

1952–56 (Ahlstrom, 1959, p. 204). Furthermore, a coincidence of distributions of parent stocks and their eggs was detected in the related species, *Sardinops melanosticta*, inhabiting the waters adjacent to Japan (Nakai, 1960, p. 821).

SUMMARY

The rate of natural mortality of the Pacific sardine seems to be higher in the older fish than in the younger ones and higher in the southern subpopulation than in the northern one. For this reason it is indicated that natural mortality should be estimated for the subpopulations by age from the catch data of two adjacent age groups.

Availability was found to differ by age as well as by season. High correlations were obtained between the rates of two adjacent age groups exploited in the same fishing season; therefore, this rate also should be estimated by examination of two adjacent age groups.

The data suggest that availability was positively correlated with water temperatures in July to September, immediately preceding the fishing season.

In addition to the above factors, others such as efficiency of gear and area of fishing grounds may affect the catch curves. The most promising procedures may be the comparisons of the total mortality coefficients, number of boats, and area of fishing grounds during the shortest time periods. Consideration of these facts indicates that running averages for six seasons should be computed for these factors.

ACKNOWLEDGMENTS

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DIEL MOVEMENT AND VERTICAL DISTRIBUTION OF JUVENILE ANADROMOUS FISH IN TURBINE INTAKES

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ABSTRACT

The behavior of fingerling salmonids was measured in turbine intakes of The Dalles and McNary Dams on the Columbia River to aid in developing methods for reducing fish mortality in Kaplan turbines. At The Dalles Dam, diel movement and vertical distribution were sampled at both ends and at the middle of the section of the powerhouse that housed turbines 1 through 12. At McNary Dam, vertical distribution was sampled in intake 12–C, located near the middle of the River channel.

Comparisons of day-night occurrence at The Dalles Dam showed that most chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), and ammocoetes of the Pacific lamprey (*Lampetra tridentata*) were caught at night (7 p.m. to 7 a.m.). Vertical distribution studies at McNary and The Dalles Dams included catches of sockeye salmon (*O. nerka*) in addition to the above species. Salmonids were taken at all depths, but most were in the upper 30 percent of water in the intakes (within 4.6 m. of the ceiling). Ammocoetes at The Dalles Dam (no data for McNary Dam) were concentrated near the center and bottom of the intakes; very few were near the ceiling.

To increase survival of fish by manipulating turbine loads during a 24-hour operational period appears feasible. During darkness when fish movements through turbines increase and power demands decrease, the reduction in turbine loads improves the flexibility for adjusting turbine loads to increase fish survival.

The concentration of fingerling salmonids near intake ceilings probably causes most of the fish to pass the turbine runner at or near the hub; therefore, methods for eliminating lethal factors at the runner should be applied first at the hub. In addition, use of deflection and bypass techniques near intake ceilings would be advantageous because the concentration of fish is greatest there.

The behavior of fingerling salmonids in turbine intakes, including their time of passage and distribution in the water mass, can profoundly influence development of efficient and economical methods for reducing fish mortality in turbines. The need for fish protection at dams is becoming particularly acute in the Columbia Basin because the progeny of upriver stocks of salmonids soon will be forced to pass through the turbines of 8 to 10 dams to reach the sea.

At present, normal spring flows are divided about equally between spillways and turbines; numbers of young fish migrating downstream presumably pass through the spillways and the turbines in proportion to the water passed by each. Studies at McNary and Big Cliff Dams under normal operating conditions (wicket gates opened 75–80 percent) have shown that mortality of young salmon in Kaplan turbines is about 11 percent, whereas mortality in the spillway is comparatively light—2 percent (State of Washington Department of Fisheries;[1] Schoeneman, Pressey, and Junge, 1961). Similar mortality is assumed to occur at other dams with comparable turbine designs and operational features.

Unless solutions are found, the total mortality will increase in the future. When the Corps of Engineers' Projects are completed, almost all water in the Columbia Basin's flow regime eventually will pass through turbines, eliminating the relatively safe passageway now provided by water

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[1] State of Washington Department of Fisheries. Research relating to mortality of downstream migrant salmon passing McNary and Big Cliff Dams. Progr. Rep. Fish. Eng. Res. Program, 1960, N. Pac. Div., U.S. Army Corps Eng., pp. 122–126.

flowing over the spillways. Because of the imminent danger to future runs, the Bureau of Commercial Fisheries has a research program under way to develop methods for protecting fingerlings as they pass through turbines.

From the outset of this program, knowledge of the behavior of fish immediately upstream of turbines was required. Information on diel movement was essential for obtaining more precise measures of total mortality and for estimating the feasibility of different methods for protecting fish. Research at Big Cliff Dam by the State of Washington Department of Fisheries (footnote 1) showed that mortality at two turbine loads (40 versus 80 percent wicket gate openings) differed significantly. Because turbine loads fluctuate daily, it was obvious that mortalities also might vary daily. The estimation of average daily mortality required knowledge of (1) mortality for a wide range of turbine loads, (2) daily fluctuations of turbine loads, and (3) daily variation of fish movement through turbines. If the relation of these three factors were better understood, perhaps mortality could be minimized by manipulation of turbine loads when most of the migrants are passing downstream at damsites.

Another facet of fish behavior, important to the development of protective methods, is the route used by most of the fish. Studies of models showed that flows through turbine intakes and associated scroll cases of dams such as McNary were well ordered; e.g., flows near intake ceilings pass by the top of the wicket gates, and flows near intake floors pass by the bottom of the wicket gates. Because the turbine blades lie only a few meters farther downstream, it is probable that distribution of flows at the blades corresponds with distribution of flows at the wicket gates; i.e., flows from the top of the wicket gates pass the blades at the hub, and flows from the bottom of the wicket gates pass the blades at their tips.[2] Thus, the distribution of fish at the turbine blades might be deduced with some degree of accuracy from the distribution of fish in the intakes. When fish distribution is known, meth-

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[2] Personal communication. Johnson, G. Dugan, Allis-Chalmers Manufacturing Co., York, Pa.

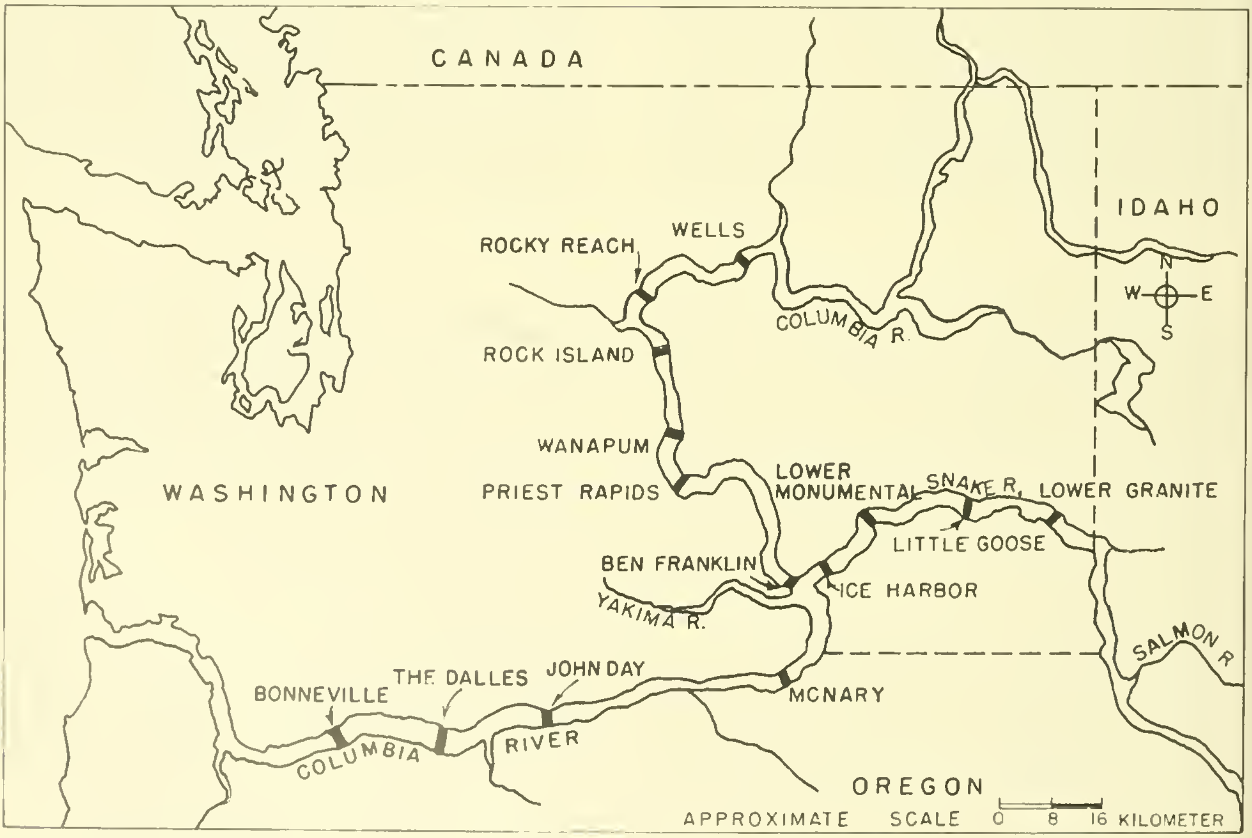
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FIGURE 1.—Location of present and future low-head dams on main stem, Columbia and Snake Rivers.

ods for eliminating lethal agents at the turbine blades can be applied at the specific area through which most of the fish pass. Knowledge of the extent of fish concentrations also can aid in determining the feasibility of guiding them into safe bypasses.

Information is available on diel movement and distribution of fingerling salmonids at several points in the river system. Mains and Smith[3] studied timing and distribution of fingerling movement in river channels; Gauley, Anas, and Schlotterbeck (1958) investigated diel movement in special bypasses at Bonneville Dam. Because the physical environment in these studies differed markedly from that in turbines and associated water passages, the data could not be applied to turbine areas with complete confidence. Additional studies accordingly were proposed.

This paper reports on experiments at two dams on the Columbia River to acquire data on timing and distribution of fingerling salmonids entering turbine intakes. In 1960, diel movement and vertical distribution of fingerling salmonids were investigated at The Dalles Dam; data on lamprey ammocoetes also were obtained. In 1961, the vertical distribution of fingerlings was studied at McNary Dam.

RESEARCH AREAS

The Dalles and McNary Dams, operated by the U.S. Army Corps of Engineers, are hydroelectric projects on the Columbia River (fig. 1) with maximum heads of 27.0 and 27.5 m., respectively. Designs and dimensions of low-head dams on the Columbia River are similar, but the powerhouses are located parallel (The Dalles) or at a right angle (McNary) to the course of the River (fig. 2).

At the times of these experiments, in 1960 and 1961, The Dalles Dam had 12 operative turbines and McNary had 14. Turbines of both Dams are equipped with three intakes—A, B, and C. Each intake has a gatewell, or vertical shaft, which extends from an opening in the ceiling of the intake to the forebay deck. Figure 3 is a cross section of an intake at The Dalles Dam, showing the gatewell and other features. The turbines and turbine intakes of McNary Dam have a similar design.

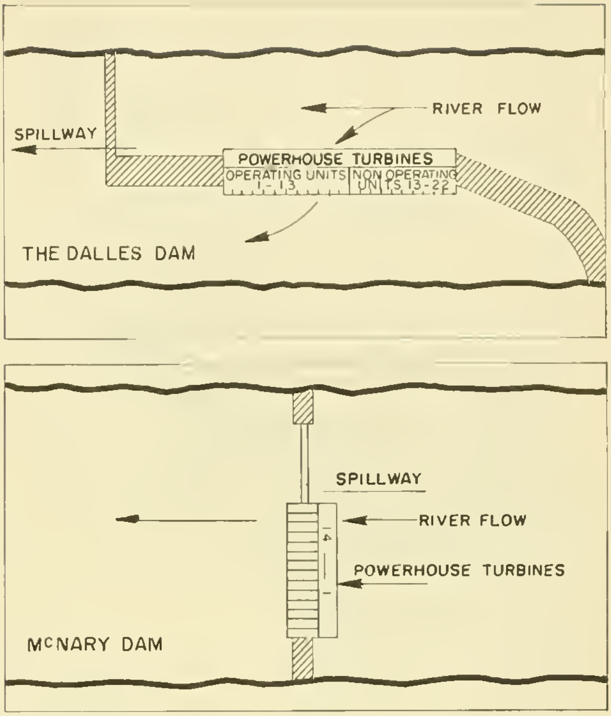

FIGURE 2.—Comparison of The Dalles and McNary Dams. The orientation of the powerhouse of The Dalles Dam, nearly parallel to the course of the River, causes water to turn nearly 90° to pass through turbines. The powerhouse of McNary Dam is oriented at right angles to the course of the River.

DESIGN AND OPERATION OF SAMPLING APPARATUS

A special intake frame supporting six fyke nets (fig. 4) was used to capture fingerlings passing through turbine intakes at The Dalles and McNary Dams. The fyke nets were installed one above the other in the frame. When the frame was installed in the intake, the nets extended from the ceiling of the intake to within 1 m. of the floor and strained the center flows of the intake. Nearly one-third of the flow of a single intake (one-ninth of the flow of a single turbine) was strained by the six nets, discounting slightly reduced flows through the nets owing to head loss caused by the webbing.

The frame was lowered through the intake gatewell (fig. 3) with a gantry crane operated by personnel of the U.S. Army Corps of Engineers. After the frame was installed, the turbine discharge was set. Normal fluctuations in total head on the turbine produced minor changes in turbine discharge during each test. Water velocities without the nets

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[3] Mains, J. E., and J. M. Smith. Determination of normal stream distribution, size, time and current preferences of downstream migrating salmon and steelhead trout in the Columbia and Snake Rivers. Progr. Rep. Fish. Eng. Res. Program, 1956. North Pacific Division, U.S. Army Corps of Engineers, pp. 14–26.

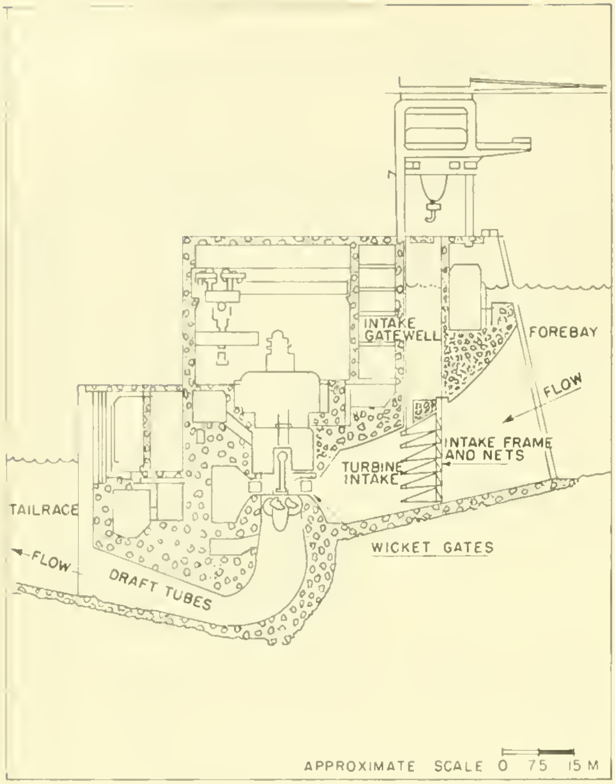

FIGURE 3.—Cross section of a main unit (turbine and associated water passages) at The Dalles Dam with intake frame in fishing position.

in place were almost the same throughout the zone strained by the nets, except for the normal boundary layer associated with the intake ceiling.[4] Therefore, all nets strained about the same amount of water.

The uppermost net was placed on the frame so the top edge of the net mouth was aligned with the intake ceiling. The frame used at The Dalles Dam was equipped with a stationary fish-tight screen extending from the top edge of the net mouth to the upstream side of the frame to provide a partial block of the opening to the gatewell (fig. 5). At McNary Dam, the frame was equipped with a hinged screen as well as a stationary screen (fig. 5). Together, the screens formed a fish-tight barrier that blocked the entire opening to the gatewell upstream from the top net.

The nets at both Dams were 1.97 m. wide by 2.13 m. high at the mouth and were 5.79 m. long, including the cod end. Fyke nets at The Dalles Dam incorporated 12.7 mm. stretched mesh nylon webbing in the forward half of the body and 9.5 mm. stretched mesh nylon in the back half. At The Dalles, the smaller mesh tended to plug up with fine vegetable debris; the difficulty was alleviated at McNary Dam by constructing fyke nets entirely of 12.7 mm. stretched mesh. Cod ends of the nets at both Dams were of 3.2 mm. nylon bobbinet.

Procedure was the same at both Dams. Before the frame was lowered to fishing position, each net was folded and tied to the frame with string that could be broken easily by flows in the turbine intake. Flows were stopped before the frame was lowered or raised to prevent capture of fish while the nets were moving up or down. At the end of each fishing period, the intake frame was hauled to deck level, and the contents of each net were emptied into separate containers for sorting and counting.

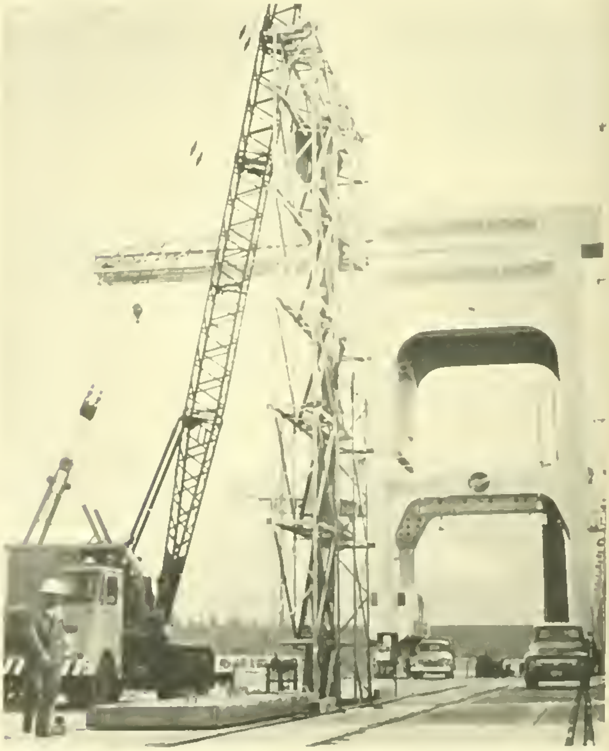

FIGURE 4.—Intake frame being lowered through gatewell into a turbine intake at McNary Dam. Frame supports fyke nets used to measure diel movement and vertical distribution of fingerling salmonids approaching Kaplan turbines.

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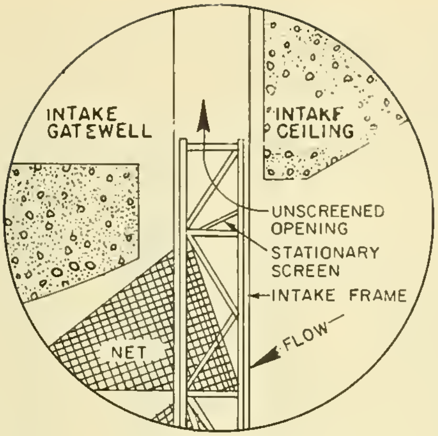
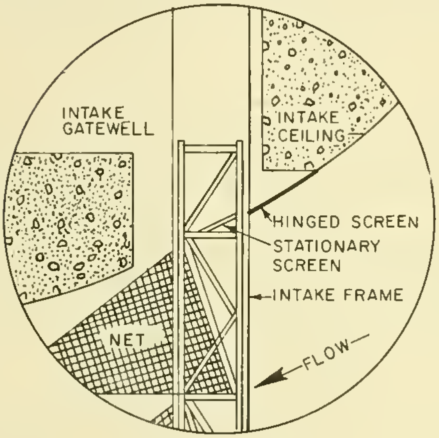
[4] Unpublished data furnished by U.S. Army Corps of Engineers, North Pacific Division, Water Control Branch, 921 SW. Washington, Portland, Oreg. 97205.



THE DALLES DAM



McNARY DAM

FIGURE 5.—Upper portions of intake frame in fishing position at The Dalles Dam and McNary Dam. Note hinged screen used at McNary Dam to ensure that fish near the ceiling of the intake did not escape the top net by swimming up into the gatewell.

DESIGN OF EXPERIMENTS

Experiments at The Dalles Dam measured (1) diel movement and (2) vertical distribution of fingerling salmonids in the turbine intakes. An additional experiment provided information on the vertical distribution of fingerlings at McNary Dam.

THE DALLES DAM EXPERIMENTS

In both experiments at The Dalles Dam, the fyke nets were fished in the center intake (B) of turbines at both ends and at the middle of the part of the powerhouse that contained operating turbines. Turbines 1 to 10 operated continuously; turbines 11 and 12 operated intermittently; turbines 13 through 22 had not been installed. At the beginning of each fishing period, the turbine was set to discharge about 310 c.m.s. (cubic meters per second), producing a water velocity of about 1.2 m.p.s. (meters per second) in the zone strained by the nets (measured without the nets in place). The gatewell involved during a test was uncovered for the entire test period.

The salmonids were classified into two major size groups. Fish in the smaller group (under 80 mm. fork length) were termed O-group, or first year of life. Periodic examinations indicated this group was composed almost exclusively of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Fish 80 mm. and longer were classed as I-group (second year of life or more) and identified by species. Catches of I-group salmonids during the experiment on diel movement included chinook salmon and steelhead trout (*Salmo gairdneri*). Ammocoetes of the Pacific lamprey (*Lampetra tridentata*) also were caught. Catches made during the study of vertical distribution included I-group sockeye salmon (*O. nerka*) in addition to the species mentioned above.

The first experiment (April 7–27, 1960) consisted of 18 tests to study diel movement of juvenile salmonids in turbine intakes. Each test was composed of one day- and one night-fishing period in the same intake within a single 24-hour period. Day fishing averaged 10¼ hours within the 12-hour period, 7 a.m. to 7 p.m. Night fishing averaged 10¼ hours within the 12-hour period, 7 p.m. to 7 a.m. Tests in each area of the powerhouse were made at 2- to 6-day intervals, conditions permitting. Five tests were made at unit 1, seven at unit 5, and six at units 10 and 11 (fig. 2).

In the second experiment (April 28 to May 12, 1960), 14 tests were made to sample the vertical distribution of fingerling salmonids. Each test was composed of a single fishing period, averaging 16 hours within the 17-hour period from 3:30 p.m. to 8:30 a.m.[5] Tests were made in each of three areas of the powerhouse: five in unit 1, six in units 5 and 6, and three in units 10 and 12. Tests in a single area were spaced at least 3 days apart.

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[5] This fishing period was chosen to allow personnel of the U.S. Army Corps of Engineers to install and remove the intake frame without seriously disrupting their normal work schedule.

McNARY DAM EXPERIMENT

One set of 10 tests was completed at McNary Dam (April 24 to May 26, 1961) to determine the vertical distribution of juvenile salmonids. Each test covered a single 8-hour fishing period, beginning at 7 p.m. and ending at 5 a.m. Tests were run only in intake C of unit 12, which is near the center of the River channel. At the beginning of each test, the turbine discharge was set at 354 c.m.s., producing a water velocity of about 1 m.p.s. in the zone strained by the nets, as measured without the nets in place (footnote 4). Tests were run in pairs (2 consecutive days) with 6 nights between each pair. The gatewell was uncovered for the duration of the experiment.

The O-group salmonids were scarce: only I-group chinook and sockeye salmon and I-group steelhead trout were taken in sufficient numbers for analysis. Some ammocoetes were caught, but the data are not included here.

RELIABILITY OF CATCH DATA

Three major factors could have affected the reliability of the catch data: (1) different fishing efficiency of the fyke nets between day- and night-fishing periods, (2) capture of fish as the nets were drawn up through the water in the gatewells, and (3) avoidance of the top net at The Dalles Dam by fish that entered the gatewell before reaching the net.

Efficiency of the fyke nets could have varied if fish were able to see the nets better during the day than during the night. Recent experiments in the Snake River below Brownlee Dam indicated this possibility. Sims (unpublished)[6] found that "scoop traps" were three times more efficient in capturing marked fish at night than during the day. Because vertical distribution of the fish was constant, he suggested that lessened visibility may have been responsible for the higher trap efficiencies at night. Illumination within the turbine intakes was not measured during tests reported here, but Secchi disc readings ranged from 0.43 to 0.85 m. at The Dalles Dam. In addition, the fyke nets were located within the turbine intake (about 15 m. downstream from the mouth) under more than 20 m. of water (vertical distance through the water in the gatewell). The turbidity and the location of the nets indicated that illumination was probably not much higher during the day than during the night. It seems unlikely that fish were able to see the nets well during either day or night.

Recognizing that fish might be caught as the nets were drawn up through static water in the gatewells, I examined the physical condition of the fish to determine where they were caught. Prior experience had proven that fish would be dead and extensively descaled when caught by nets in water velocities equal to those in the turbine intakes. I reasoned that because water in the gatewell was not flowing, fish from nets raised slowly through the gatewell would be alive and suffer no more harm than would be caused by a dip net. Few live fish were taken during the experiment; when present, they were excluded from the catch data.

The catches made in the top net at The Dalles Dam may not have been indicative of the actual number of fish in that area because some may have escaped by swimming into the gatewell through the unscreened opening upstream from the net. Modifications of the intake frame precluded avoidance of the top net at McNary Dam.

Available information concerning the three points discussed in this section leads me to believe that the catch data depict reliably the general behavior of fish in turbine intakes. Experimental equipment and procedures that can circumvent these potential sources of error are nevertheless desirable for future experiments.

DIEL MOVEMENT

Data on diel movement of migrating juvenile salmonids in turbine intakes (intake B of units 1, 5, 10, and 11) at The Dalles Dam are presented in table 1. Occurrence by age groups and species is presented graphically in figure 6.

The following conclusions seem to be warranted:

1. Day and night passage for all age groups and species did not differ significantly among intakes sampled (at both ends and the middle of the row of operating turbines).
2. Although all age groups and species were more abundant at night than during the day, only the I-group salmonids were significantly more plentiful.
3. Of the I-group chinook salmon and I-group steelhead trout, 94 and 85 percent, respectively,

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[6] Sims, Carl W. Escapement of juvenile salmonids from Brownlee Reservoir. Fish-Passage Research Program, Bureau of Commercial Fisheries, Seattle, Wash. Manuscript in preparation.

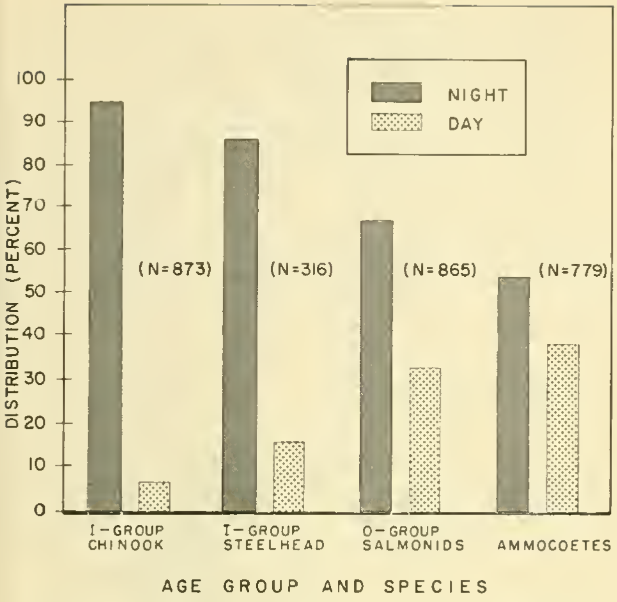

FIGURE 6.—Comparison of day (7 a.m. to 7 p.m.) and night (7 p.m. to 7 a.m.) catches of juvenile anadromous fish in turbine intakes of The Dalles Dam. Results of 18 tests, April 7–27, 1960.

TABLE 1.—*Diel movement of fingerling salmonids and lamprey ammoeoetes in turbine intakes of unit 1 (downstream end), unit 5 (center), and units 10 and 11 (upstream end of powerhouse) at The Dalles Dam*

[Results of 18 tests, April 7–27, 1960]

Age groups and species	Catch by powerhouse area [1]								
	Downstream end			Middle			Upstream end		
	Night	Day	Total	Night	Day	Total	Night	Day	Total
	Percent	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*
I-group chinook salmon	94.4	5.6	358	94.2	5.8	189	93.9	6.1	326
I-group steelhead trout	89.8	10.2	118	82.7	17.3	127	81.7	18.3	71
O-group salmonids	61.2	38.8	201	62.5	37.5	248	71.7	28.3	416
Ammocoetes	63.5	36.5	315	51.1	48.9	282	75.8	24.2	182

[1] See figure 2 for location.

were caught at night. Of the O-group salmonids and ammocoetes, 67 and 62 percent, respectively, were caught at night.

Results reported here agree generally with those of other investigators of day and night movement of fingerlings. In the undammed sections of the Snake and Columbia Rivers, most of the I-group chinook salmon and I-group steelhead trout were captured from 6 p.m. to 6 a.m. (Mains and Smith, footnote 3). In research in special bypasses at Bonneville Dam, Gauley et al. (1958) found significantly more O-group chinook salmon, I-group chinook salmon, and I-group steelhead trout migrating from 6 p.m. to 6 a.m. in 4 out of 5 seasons—1946, 1949, 1950, and 1953. More recently, Monan, McConnell, Pugh, and Smith (unpublished) [7] caught a majority of salmonid fingerlings (mixed species) between 8 p.m. and 6 a.m. in the Snake River.

VERTICAL DISTRIBUTION

Vertical distribution of juvenile anadromous fish migrating through turbine intakes of The Dalles Dam (intake B of units 1, 5, 6, 10, and 12) and of McNary Dam (intake C of unit 12) is presented in tables 2 through 8 and figures 7 and 8.

TABLE 2.—*Vertical distribution of O-group salmonids in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0– 2.1	88	30.4	111	31.6	107	24.6
2	2.3– 4.4	42	14.5	70	19.9	93	21.4
3	4.6– 6.7	41	14.2	49	14.0	76	17.5
4	6.9– 9.0	43	14.9	63	18.0	81	18.7
5	9.2–11.3	32	11.1	40	11.4	62	14.3
6	11.4–13.6	43	14.9	18	5.1	15	3.5
Total		289	100.0	351	100.0	434	100.0

[1] From ceiling of intake at gatewell.

TABLE 3.—*Vertical distribution of I-group chinook salmon fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0–2.1	321	55.9	211	45.8	51	35.2
2	2.3– 4.4	131	22.8	113	24.5	46	31.7
3	4.6– 6.7	62	10.8	67	14.5	29	20.0
4	6.9– 9.0	25	4.4	36	7.8	13	9.0
5	9.2–11.3	17	3.0	24	5.2	5	3.4
6	11.4–13.6	18	3.1	10	2.2	1	.7
Total		574	100.0	461	100.0	145	100.0

[1] From ceiling of intake at gatewell.

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[7] Monan, Gerald E., Robert J. McConnell, John R. Pugh, and Jim R. Smith. Distribution of downstream migrant salmonids and the study of debris in the Snake River above Brownlee Reservoir. Fish-Passage Research Program, Bureau of Commercial Fisheries, Seattle, Wash. Manuscript in preparation.

TABLE 4.—*Vertical distribution of I-group steelhead trout fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0- 2.1	66	44.9	87	46.3	9	56.3
2	2.3- 4.4	39	26.6	51	27.1	3	18.7
3	4.6- 6.7	19	12.9	25	13.3	3	18.7
4	6.9- 9.0	9	6.1	18	9.6	0	0
5	9.2-11.3	8	5.4	3	1.6	1	6.3
6	11.4-13.6	6	4.1	4	2.1	0	0
Total		147	100.0	188	100.0	16	100.0

[1] From ceiling of intake at gatewell.

TABLE 5.—*Vertical distribution of I-group sockeye salmon fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0- 2.1	70	36.6	52	26.1	17	50.0
2	2.3- 4.4	47	24.6	54	27.2	6	17.6
3	4.6- 6.7	31	16.2	37	18.6	3	8.8
4	6.9- 9.0	20	10.5	33	16.6	4	11.8
5	9.2-11.3	15	7.9	8	4.0	2	5.9
6	11.4-13.6	8	4.2	15	7.5	2	5.9
Total		191	100.0	199	100.0	34	100.0

[1] From ceiling of intake at gatewell.

TABLE 6.—*Vertical distribution of lamprey ammocoetes in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0- 2.1	52	8.0	36	4.9	13	4.4
2	2.3- 4.4	98	15.1	92	12.4	19	6.5
3	4.6- 6.7	128	19.7	142	19.3	41	14.0
4	6.9- 9.0	154	23.7	171	23.2	62	21.2
5	9.2-11.3	167	25.8	204	27.7	89	30.4
6	11.4-13.6	50	7.7	92	12.5	69	23.5
Total		649	100.0	737	100.0	293	100.0

[1] From ceiling of intake at gatewell

TABLE 7.—*Vertical distribution of fingerling salmonids in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.*

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth [1]	All species and age groups	
	M.	*Number*	*Percent*
1	0- 2.1	1,190	39.3
2	2.3- 4.4	695	22.9
3	4.6- 6.7	442	14.6
4	6.9- 9.0	345	11.4
5	9.2-11.3	217	7.2
6	11.4-13.6	140	4.6
Total		3,029	100.0

[1] From ceiling of intake at gatewell.

TABLE 8.—*Vertical distribution of fingerling salmonids in turbine intake 12-C at McNary Dam. Combined results of 10 tests extending from 7 p.m. to 5 a.m.*

[Test period, April 24 to May 26, 1961]

Net number (top to bottom)	Depth [1]	Age group and species						Total	
		I-group chinook		I-group steelhead		I-group soekeye			
	M.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	0- 2.1	351	56.7	47	54.0	104	33.6	502	49.4
2	2.3- 4.4	140	22.6	17	19.5	89	28.7	246	24.2
3	4.6- 6.7	74	12.0	16	18.4	46	14.8	136	13.4
4	6.9- 9.0	33	5.3	5	5.8	35	11.3	73	7.2
5	9.2-11.3	12	1.9	2	2.3	22	7.1	36	3.5
6	11.4-13.6	9	1.5	0	0	14	4.5	23	2.3
Total		619	100.0	87	100.0	310	100.0	1,016	100.0

[1] From ceiling of intake at gatewell.

Catches at The Dalles Dam showed:

1. Vertical distribution of salmonids did not vary among areas of the powerhouse sampled; therefore, the catch data for all intakes were combined for subsequent analysis.

2. The combined catches of all salmonid species and age groups showed that most were caught in the top two of the six nets.

3. The I-group chinook salmon and I-group steelhead trout were most strongly concentrated in the top two nets—73 and 74 percent, respectively.

4. The O-group chinook salmon and I-group sockeye salmon were less strongly concentrated in the top two nets—48 and 58 percent, respectively.

5. The vertical distribution of ammocoetes was the reverse of that of salmonids; very few were caught in the top two of the six nets. This distribution held for all areas of the powerhouse. The zone of highest concentration at the upstream end

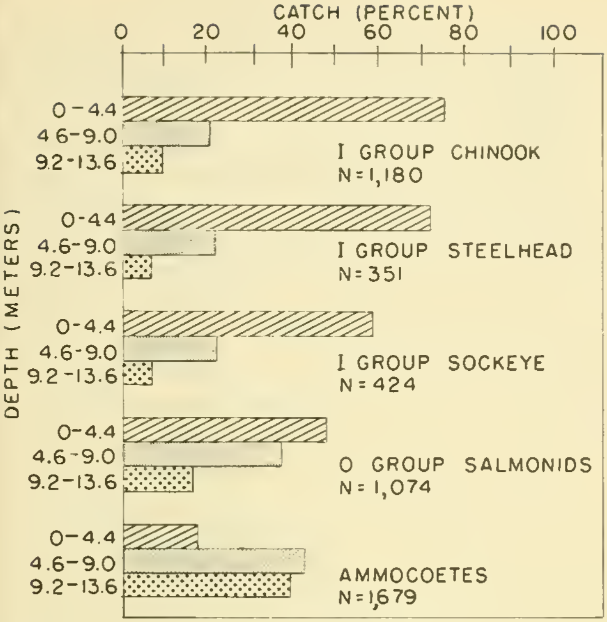

FIGURE 7.—Combined results of 14 tests showing vertical distribution of juvenile anadromous fish in turbine intakes of The Dalles Dam. Each 16-hour test was between 3:30 p.m. and 8:30 a.m. Test period, April 28 to May 12, 1960.

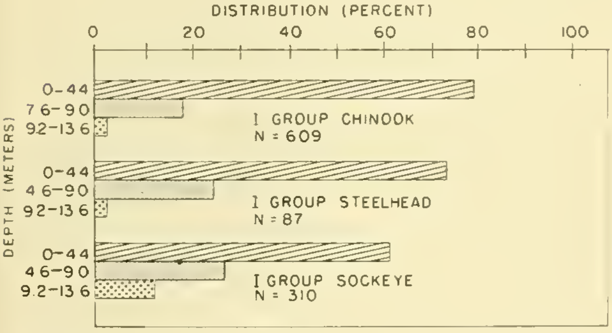

FIGURE 8.—Combined results of 10 tests showing vertical distribution of fingerling salmonids in intake 12-C at McNary Dam. Each 8-hour test was between 7 p.m. and 5 a.m. Test period, April 24 to May 26, 1961.

of the powerhouse occurred in the bottom two of the six nets, whereas the zone of highest concentration was in the two center nets in the center and downstream end of the powerhouse. This difference was statistically significant.

Catches at McNary Dam showed that the vertical distribution of I-group chinook and sockeye salmon and I-group steelhead trout was much the same as the vertical distribution of these age groups and species at The Dalles Dam. The I-group chinook salmon and steelhead trout were most strongly concentrated in the top two nets (79.3 and 73.5 percent, respectively), whereas I-group sockeye salmon were somewhat less concentrated (62.3 percent).

IMPLICATIONS OF RESEARCH IN TURBINE INTAKES

Information on diel movement and vertical distribution of fingerling salmonids in turbine intakes applies directly to the problem of developing methods for reducing fingerling mortality in Kaplan turbines. Important implications are discussed below.

DIEL MOVEMENT

According to past research, day and night movement of fish can vary significantly from year to year, presumably because of changes in turbidity and other facets of water quality. Mains and Smith (footnote 3) caught 57 percent of the I-group chinook salmon at night in the Snake River in 1954, whereas in 1955 they caught 78 percent at night. Gauley et al. (1958) caught significantly more O-group chinook salmon and I-group steelhead trout in special bypasses at Bonneville Dam during the night in 4 of 5 seasons; but in 1952, significantly more of these species were caught by day. Data by Gauley et al. (1958) suggested that turbidity may have influenced timing of fish movement. In view of past research, the data on day and night movement reported here should be applied with some reservation because continuing development of the river system may well alter water quality, including turbidity, in the future.

Although data on day and night movement must be considered only partially complete, the results—especially for I-group fingerlings—suggest a fortunate relation between timing of fish passage at dams and the normal schedule of turbine loading. Night movement of fish through turbines favors higher rather than lower average survival. At night the decreased demand for power causes reduced turbine loads. Preliminary information recently obtained at Big Cliff Dam[8] indicates that survival is highest at highest turbine efficiencies. Peak efficiency is achieved at reduced turbine loads, typically near 70 percent of maximum rated capacity.[9]

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[8] Oligher, Ray. Fish passage through turbines—tests at Big Cliff hydroelectric plant. U.S. Army Corps of Engineers, North Pacific Division, Walla Walla District, Walla Walla, Wash. Letter report (1965), 14 pp.

Reduced power demand also increases flexibility for adjusting turbine loads to maximize fish survival—shifting of load demand from turbines where fish passage is high to turbines where fish passage is low (between turbines in a given dam and between dams in the same power-grid system). The potential increase in fish survival that might be achieved by using this technique, however, cannot be estimated with accuracy from available data. Among other requirements, timing of fish movement should be determined for shorter periods of time, especially for dawn and dusk. Peaks are expected at dawn and dusk (Mains and Smith, footnote 3; Gauley et al., 1958; Monan et al., footnote 7) and the demand for power fluctuates during these hours of the day.

VERTICAL DISTRIBUTION

Data on vertical distribution have helped define more precisely the direction that future research should take to develop suitable protective methods. Most fingerlings in turbine intakes of both The Dalles Dam and McNary Dam are in flows near the ceiling of the intake. These flows pass the turbine blades at or near the hub (G. D. Johnson, footnote 2). If fish remain in these flows, they also must pass the blades near the hub. Protective methods designed to eliminate or nullify the effects of lethal agents, therefore, should be used first at the hub of the runner. These data also imply that most salmonid fingerlings could be routed into safe bypasses if a guiding system were designed to remove fish only from the upper 4.6 m. of water within turbine intakes.

SUMMARY

1. A frame supporting six fyke nets was used to measure diel movement and vertical distribution of fingerling chinook salmon, sockeye salmon, steelhead trout, and ammocoetes of the Pacific lamprey in turbine intakes at The Dalles Dam (1960) and McNary Dam (1961).

2. The nets were positioned one above the other in the frame and extended from the intake ceiling to within 1 m. of the floor to strain the center third of flows in a single intake (one-ninth of total turbine discharge).

3. Diel movement for all age groups and species did not differ significantly between areas of the powerhouse at The Dalles Dam. Although all age groups and species were more abundant at night (7 p.m. to 7 a.m.) than during the day (7 a.m. to 7 p.m.), only the I-group salmonids were significantly so. The night catches of I-group chinook salmon and I-group steelhead trout were 94 and 85 percent of the total, respectively, whereas the night catches of O-group salmonids and ammocoetes were 67 and 62 percent of the total, respectively.

4. Vertical distribution of salmonids did not vary between areas of the powerhouse sampled at The Dalles Dam. At both Dams, most I-group fingerlings were concentrated in the top two of six nets, or within 4.6 m. of the ceiling of the turbine intakes. At The Dalles and McNary Dams, respectively, the results for I-group chinook salmon were 73 and 79.3 percent; for I-group steelhead trout, 74 and 73.5 percent; and for I-group sockeye salmon, 58 and 62.3 percent. O-group salmonids were less strongly stratified than I-group fingerlings: 48 percent were caught in the top two nets.

5. Vertical distribution of ammocoetes at The Dalles Dam was the reverse of that for salmonids: few were taken in the top two nets.

6. Predominantly night movement of fingerlings through turbines favors higher rather than lower survival because (a) survival is highest at reduced loads near 70 percent of maximum rated capacity and (b) reduction in demand for power at night results in lower turbine loads. Reduced turbine loads also make it possible to shift loads from turbines where fish passage is greatest to those where fish passage is least, thus increasing total fish survival.

7. The concentration of fingerlings near the ceilings of intakes implies that most fish pass through the Kaplan runners at or near the hub. It follows that methods for eliminating the effects of lethal agents at the runner should be applied first at the hub. In addition, use of deflection and bypass techniques near intake ceilings would be advantageous because the concentration of fish is greatest in this region.

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[9] Hydraulic plant operator training manual, Part II, U.S. Army Corps of Engineers, North Pacific Division, Portland, Oreg. 22 pp.

ACKNOWLEDGMENTS

The aid and cooperation of Glen Blegen and Herbert Ewing of The Dalles Dam and Dwayne Downing, Gordon Richardson, and Verle Mendenhall of McNary Dam are greatly appreciated; the additional workload necessitated by this research was often untimely, and integration of research needs with regular work schedules was at times very difficult.

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